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DE
ZOOLOGIE

REVUE SUISSE DE ZOOLOGIE

ANNALES
DE LA
SOCIÉTÉ SUISSE DE ZOOLOGIE
ET DU
MUSÉUM D'HISTOIRE NATURELLE
DE LA VILLE DE GENÈVE



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TOME 102 — FASCICULE 1

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***Crepidobothrium eirasi* n. sp. (Cestoda: Proteocephalidae),
a parasite of the siluroid fish *Phractocephalus hemiliopterus*
(Schneider, 1801) (Pisces: Pimelodidae) from the Brazilian Amazon.**

Amilcar Arandas REGO* & Alain de CHAMBRIER**

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Crepidobothrium eirasi n. sp. (Cestoda: Proteocephalidae), a parasite of the siluroid fish *Phractocephalus hemiliopterus* (Schneider, 1801) (Pisces: Pimelodidae) from the Brazilian Amazon. - A new species of Proteocephalid cestode, *Crepidobothrium eirasi* n. sp. is described from *Phractocephalus hemiliopterus* (Schneider, 1801), a freshwater siluriform fish from the Amazon. This is the first report of *Crepidobothrium* in fish. The other known species are parasites of South American snakes. *Crepidobothrium eirasi* n. sp. is characterized mainly by their small size (with only 7-12 segments), by the notched, heart-shaped suckers, by the posterior ventral appendix of the proglottis, by the vitelline follicles, located between and external to the longitudinal muscle fibres (paramuscular), and by the absence of vitellaria in the preporal region of proglottis.

Key-words: *Crepidobothrium eirasi* n. sp. - Proteocephalidae - *Phractocephalus hemiliopterus* - (Pisces: Pimelodidae) - Brazil.

INTRODUCTION

The base of the taxonomy of the neotropical cestode family Monticelliidae parasitizing freshwater fishes was established by WOODLAND (1933a, b, c; 1934a, b, c; 1935a, b, c). The presence of a mixture of several species in his so-called type material as well as old insufficient descriptions made indispensable a collection of recent material. For this reason, the authors went to Itacoatiara, Amazonas State, Brasil (one of the Woodland's type locality) in September 1992, where numerous proteocephalideans tapeworms were collected. Among three proteocephalideans species found in the siluroid fish *Phractocephalus hemiliopterus*, one proved to belong to a new

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species and we attributed it provisionally to the genus *Crepidobothrium*. This genus comprises five species parasite of neotropical snakes (Viperidae and Boidae) (DE CHAMBRIER 1989a, b).

We found, mixed to the original material of *Myzophorus pirarara* Woodland, 1935 (parasite of the same host-species) numerous specimens of *Crepidobothrium eirasi* n. sp.

MATERIAL AND METHODS

Seven specimens of *Phractocephalus hemiliopterus* were collected and examined. They were dissected in the field immediately after death. Different portions of the entire split digestive tract were fixed with hot 4% neutral formaldehyde solution. The parasitic worms were stained with Mayer's hydrochloric carmin and with Delafield hematoxylin, then differentiated in acid alcohol, deshydrated in ethanol, cleared in Eugenol (clove oil), and mounted in Canada balsam. Transverse sections, five to twelve μm thick, were stained with Weigert's hematoxylin and counterstained with eosin. The parasites are stored in the Muséum d'Histoire naturelle, Geneva (MHNG), in the Instituto Oswaldo Cruz, Rio de Janeiro (IOC) and in the Natural History Museum, London (BMNH).

All measurements are in micrometres unless otherwise stated; Abbreviations: m = mean, n = number of measurements used, CV = coefficient of variation.

Crepidobothrium eirasi n. sp.

MATERIAL STUDIED: Brazil, Amazon river at Itacoatiara (AM), in *Phractocephalus hemiliopterus* (Schneider, 1801) 15-25.9.1992, leg A. de Chambrier & A.A. Rego: Holotype MHNG No. 992.144; 10 paratypes No. MHNG 992.145-154; one paratype IOC No. 33128; one paratype BMNH No. 1994.5.23.1; other material: slides: MHNG No. 992.155-157; 992.159-160; alcohol: MHNG No. 992.158.

Brazil, Amazon river between Manaus and Gurupa, Woodland's material, syntypes of *Myzophorus pirarara**: BMNH 1965.2.23.146-155, 1965.2.23.156-158, 1983.5.17.2-10.

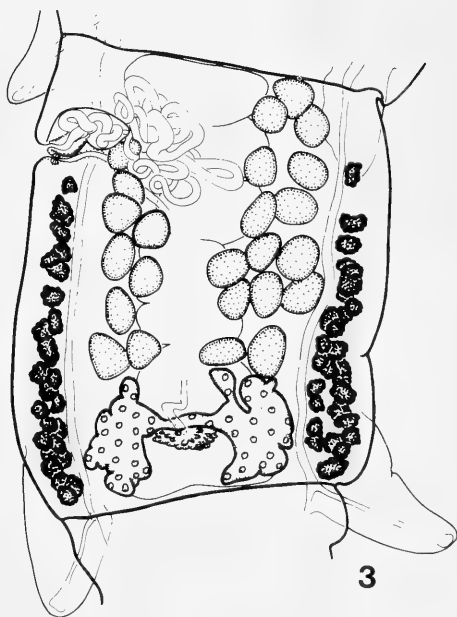
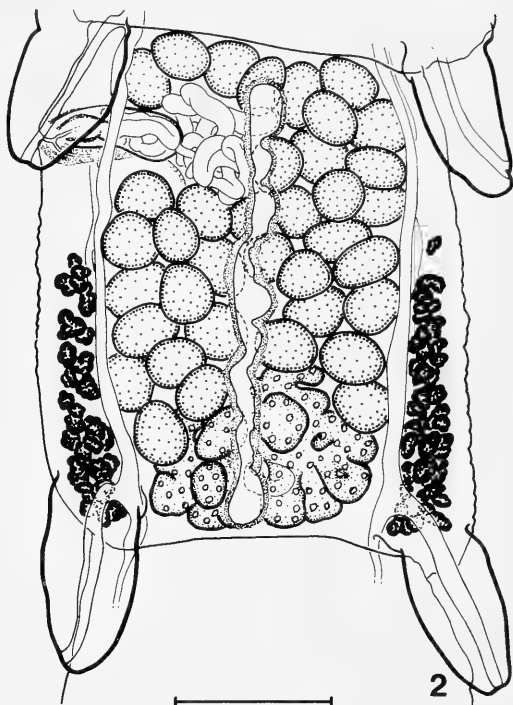
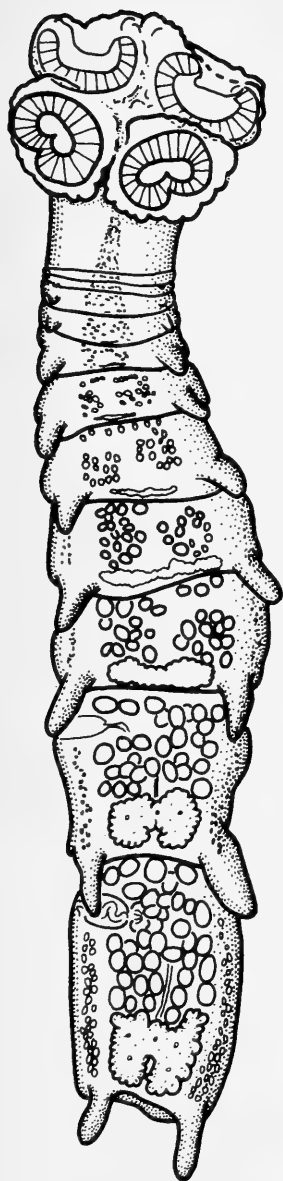
Site of infection: intestine; Prevalence: 86%, n = 7 hosts; intensity: up to more than 100 specimens.

Derivatio nominis: The new species is named in honour of Professor Jorge Eiras, from the Oporto University (Portugal) for his contribution to the knowledge of Brazilian fish pathology.

* We found, mixed to the original material of *Myzophorus pirarara* Woodland, 1935, respectively 16 specimens on slide and 75 specimens in alcohol of *Crepidobothrium eirasi* n. sp.

FIGS 1-3

Crepidobothrium eirasi n. sp. 1. Entire worm, paratype. 2. Mature proglottis, paratype, ventral view, showing the posterior appendix on each side. 3. Gravid proglottis, holotype, dorsal view. The eggs are not figured. Scale: 1 = 500 μm ; 2-3 = 250 μm .



DESCRIPTION (based on 30 specimens)

Proteocephalidae, Proteocephalinae.

Small worms, flattened dorso-ventrally. Strobila acraspedote, 2-8.5 mm long, bearing 7-12 proglottides. 100-150 long unsegmented zone posterior to scolex. Immature proglottides wider than long. Mature proglottides square or longer than wide. Gravid proglottides generally longer than wide. Proglottis with a ventral lateral posterior appendix on each side, small in immature proglottis (Figs 1, 2, 3).

Some abnormal proglottides not included in the description (e.g. with hypertrophy of vitelline follicles) were present.

Scolex massive, 495-990 in diameter, well separated from strobila, with some small apical tegumental folds (Figs 1, 9). Four prominent heart-shaped lateral suckers, opening anteriorly, with notched posterior margin, entering inside the suckorial cavity; latter 180-410 ($m = 270$, $n = 70$) in diameter (Fig. 9).

Internal longitudinal musculature weakly developed, forming bundles of lateral muscular fibres more visible on each side (Fig. 6). Ventral osmoregulatory canals 10-40 in diameter (more than 100 into the neck) with an anastomosed portion entering the posterior appendix, which seems to end at its distal surface (Figs 2, 3). Dorsal osmoregulatory canals, without anastomoses, 5-25 in diameter.

21-51 ($m = 32$, $n = 94$, $CV = 19.8$) spherical oval medullary testes in one field, extending to the osmoregulatory canals, sometimes overlapping them, reaching vitelline follicles (Fig. 2). 0-7 ($m = 3$, $n = 94$) preporal, 7-22 ($m = 12$, $n = 94$) postporal and 10-30 ($m = 17$, $n = 94$) antiporal testes, 60-70 in diameter.

Cirrus-pouch piriform, thin-walled, 120-245 long and 40-80 wide. Cirrus-pouch length to proglottis width ratio 19-38% ($m = 27\%$, $n = 28$, $CV = 15.6$). Invaginated cirrus small, 40-65 long. Cirrus occupying less than 50% of cirrus-pouch length (Fig. 5). Genitals ducts passing between the osmoregulatory canals. Ejaculatory duct long and coiled. Vas deferens coiled, occupying round field extending between proximal part of cirrus-pouch and median part of uterus, often extending over the latter in mature and gravid proglottids. Genital atrium present. Genital pores irregularly alternate, situated anteriorly between 16% and 33% ($m = 23\%$, $n = 30$, $CV = 17.2$) of proglottid length.

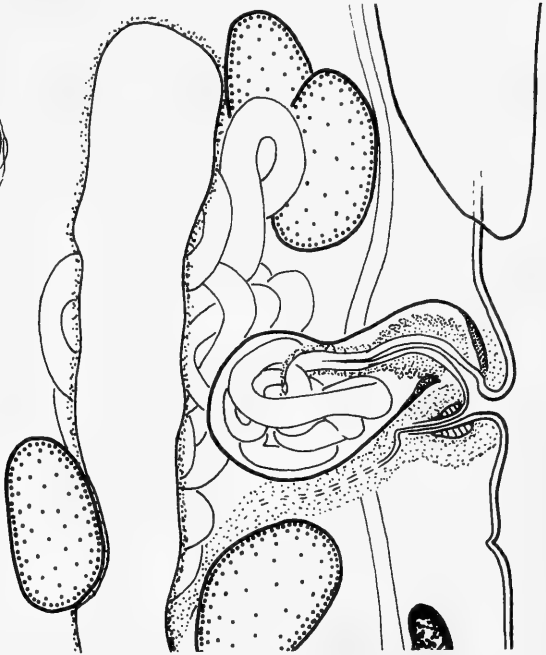
Ovary medullary, biwinged, butterfly-shaped in gravid proglottides, 210-475 wide. Ovary occupying 47-67% ($m = 57\%$, $n = 28$, $CV = 7.6$) of proglottid width (Figs 2, 3).

FIGS 4-8

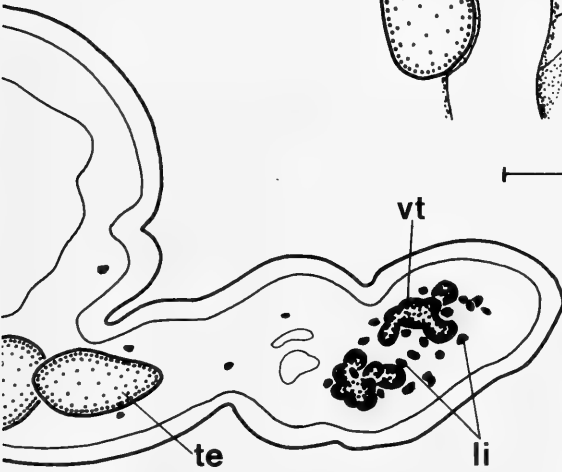
Crepidobothrium eirasi n. sp. 4. Egg showing the two internal polar circle-like structure. 5. Paratype, vagina and cirrus-pouch, pregravid proglottis, ventral view. 6. Transverse section, gravid proglottis showing the paramuscular vitellaria position. The eggs are not figured. 7. Schematic view of an egg. 8. Schematic view of a transverse section, gravid proglottis showing the distended uterus. cv = vaginal canal; dc = dorsal osmoregulatory canals; li = internal longitudinal musculature; ov = ovary; te = testes; ut = uterus; vc = ventral osmoregulatory canals; vt = vitellaria. Scale: 4 = 50 μ m; 5 = 125 μ m; 6 = 100 μ m.



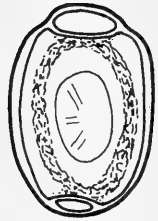
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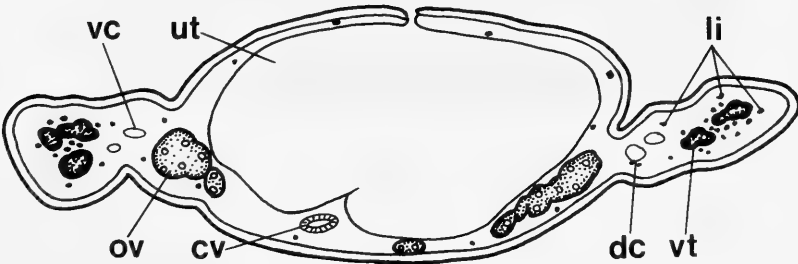
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7



8

Vagina anterior or posterior to cirrus-pouch, with an inconspicuous terminal vaginal sphincter (Fig. 5). Vagina and vaginal duct often dilated in mature proglottides. Seminal receptacle present. Mehlis' gland 80-90 in diameter. Vitelline follicles paramuscular (Figs 6, 8), i.e. located near the internal longitudinal musculature and extending into both the cortex and the medulla (see de Chambrier 1990, p. 92). Vitellaria arranged in two lateral rows, absent from the preporal region (exceptionnally one to two preporal vitelline follicles present) and from the aporally anterior part of proglottides, with a tendency to become more numerous posteriorly (Figs 2, 3). Postporal vitellaria occupying 54-81% ($m = 66\%$, $n = 22$, $CV = 9.5$) and aporal vitellaria occupying 56-86% ($m = 74\%$, $n = 20$, $CV = 11.2$) of proglottides length. Uterus preformed, developing diverticula in medulla. Uterus overlapping the ovary ventrally in immature proglottides, extending to the posterior part and occupying the entire length of gravid proglottides (Fig. 3). Uterus with 8-12 poorly marked lateral branches on each side. Uterus occupying up to 70% of the gravid proglottis width, distended in the whole median longitudinal part (Figs 6, 8). Eggs layed through one (sometimes two) precocious ventral longitudinal split occupying almost total length of proglottis.

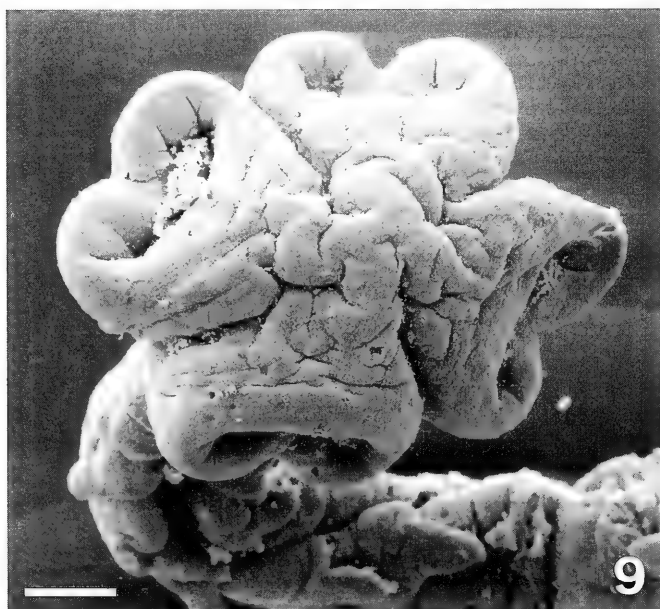


FIG. 9

Crepidobothrium eirasi n. sp. Scolex. SEM apical view, showing apical tegumental folds. Scale = 100 μ m.

Eggs with delicate external membrane, 60-70 in diameter; external envelope ovoid, 14-16 x 18-20 in diameter, with two internal similar polar structures of different diameters: 7-9 and 4-5 respectively; embryophore 11-12 x 14 in diameter, oncosphere 8-10.5 in diameter, hooks 4-5 long (Figs 4, 7).

DISCUSSION

The medullar distribution of the genital organs, the paramuscular position of vitellaria and the heart-shaped structure of suckers suggests us for the present to allocate this species, at least provisionally, in the genus *Crepidobothrium* Monticelli, 1900, (Proteocephalinae) recently revised by one of the authors (see DE CHAMBRIER 1989a, b).

The new species is characterized by the following features: suckers heart-shaped; presence of appendix at the ventral posterior edge on each side of proglottis; absence of vitellaria preporally and on anterior part of proglottis aporally; vitellaria paramuscular; uterus occupying the entire length of immature proglottis; eggs with two internal polar structures of different diameters.

The present new species differs from the five known species in this genus (*Crepidobothrium gerrardii* (Baird, 1860) parasite of *Boa constrictor*; *C. dollfusi* Freze, 1965 and *C. lachesidis* MacCallum, 1921, parasites of *Eunectes murinus*; *C. viperis* (Beddard, 1913) and *C. garzonii* de Chambrier, 1988, parasites of *Bothrops alternatus*) (BAIRD 1860; BEDDARD 1913; DE CHAMBRIER 1988; FREZE 1965; MACCALLUM 1921) by the following characters: Absence of apical organ, presence of appendix at the ventral posterior edge on each side of proglottis, absence of preporal vitellaria, egg structure, smaller number of testes, small size of strobila.

C. eirasi n. sp. is the only species of the order Proteocephalidea having posterior ventral appendices on each proglottis. This structure is certainly not homologous with the overlapping of the posterior border of proglottis (craspedote morphology). WOODLAND (1935a), in his description of *Myzophorus pirarara*, did not mention the presence of appendices, in spite of the fact that specimens of *C. eirasi* n. sp. were present in his type material.

The absence of preporal vitellaria is rare in neotropical Proteocephalidae. Only *Proteocephalus sophiae* de Chambrier & Rego, 1994 from *Paulicea luetkeni* and *P. macdonaghi* (Szidat & Nani, 1951) from *Basilichthys microlepidotus* share this character with *C. eirasi* n. sp. (DE CHAMBRIER & REGO 1994; SZIDAT & NANI 1951).

The two internal polar ovoid structures of the eggs are unusual in proteocephalid cestodes. These structures look like two opercules, but a careful observation shows that they are located in the internal part of the external envelope.

The catfish *Phractocephalus hemiliopterus* has been recorded, up to now in the Amazon basin, as host of the four following species: *Zygobothrium megacephalum* Diesing, 1850, *Nomimoscolex pirarara* (Woodland, 1935) (= *Myzophorus pirarara* Woodland, 1935) and *Nomimoscolex woodlandi* (Rego, 1984) (= *Myzophorus woodlandi* Rego, 1984) (see REGO & PAVANELLI 1992a, b). *Crepidobothrium eirasi* n. sp. is the fifth Proteocephalidea described from this host species.

The weak longitudinal musculature is a common character to three species parasite of *Phractocephalus hemioliopterus*. Such a weak musculature makes it more difficult to determine of the medullar or cortical position of vitellaria, which characterize respectively the Proteocephalinae and the Zygobothriinae. In the beginning of the discussion, we expressed a reserve about the allocation of our species in the genus *Crepidobothrium*, and consequently in the Proteocephalinae, due to the intermediate position of vitellaria. The heart-shaped structure of the suckers was decisive to place *C. eirasi* n. sp. in the genus *Crepidobothrium*.

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RESUMO

É descrita uma nova espécie de proteocefalídeo, *Crepidobothrium eirasi* sp. n., parasita do peixe siluriforme pimelodídeo, *Phractocephalus hemioliopterus*. É a primeira referência de *Crepidobothrium* em peixes; as outras espécies foram descritas de serpentes da América do Sul. *C. eirasi* sp. n. pode ser caracterizada pelas suas reduzidas demensões (apenas 7-12 segmentos), pelas ventosas cordiformes, pelos apêndices do bordo posterior dos proglotes, pela distribuição dos folículos vitelinos, situados entre as fibras musculares e também externamente as mesmas, (paramuscular), além da ausência de vitelinos na região preporal dos proglotes.

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The influence of air pollution on moss - dwelling animals:
5. Fumigation experiments with SO₂ and exposure experiments

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The influence of air pollution on moss - dwelling animals: 5. Fumigation experiments with SO₂ and exposure experiments. - This study focused on long-term exposure of moss-dwelling test communities with relatively low pollution ratings. Changes in the composition of the aquatic fauna (i.e. rotifers, nematodes and tardigrades) were correlated with SO₂ concentrations in a fumigation experiment and to the air quality of 12 sites in the exposure experiments. Moss-growing tiles were transferred in groups of four either to fumigation chambers or to exposure sites. Three levels of SO₂ (0.025, 0.075 and 0.225 ppm) plus untreated control mosses were used in the fumigation experiments that lasted 18 months. The highest SO₂ level caused significant reduction in the numbers of several nematode and tardigrade species. At intermediate concentrations of SO₂, both positive and negative responses to fumigation were observed by individual species. Fumigation with SO₂ significantly decreased pH in the moss cushions. The final response of the transplanted fauna in the exposure experiments resulted from an interaction of air pollutants and various environmental variables. Some exposure sites were "without" any observed effects whereas others had severe effects, which include the disappearance of many species. Large differences in susceptibility to the different exposure conditions were observed. Populations of *Chiloplectus* cf. *andrassyi* and *Paratripyla intermedia* decreased with increasing pollution, whereas populations of *Macrobiotus persimilis* increased. These species are considered suitable indicators of air pollution.

Key-words: Moss-invertebrate associations - Fumigation experiment - Sulfur dioxide - Exposure experiment - Biological indicator - Air pollution.

1 INTRODUCTION

Detailed studies dedicated to air pollution effects on the soil environment and associated flora and fauna are scarce. The present paper is part of a study investigating the influence of air pollution on moss-dwelling animals in the region of Zürich (Switzerland). A survey of natural moss-dwelling communities revealed that several taxa are sensitive to pollution (STEINER, 1994b, 1995). Since the fauna of moss cushions is available for study in situ or manipulation, and is similar to the fauna of soils (NICHOLAS, 1984), it could act as an indicator system of air pollution effects on soil ecosystems. To assess the suitability of the moss-dwelling fauna as an indicator of air pollution, fumigation and field experiments were performed using standardised aquatic communities (i.e. rotifers, nematodes and tardigrades). A major advantage of these experiments vis-a-vis the survey of natural communities is that a species presence or absence at a given site cannot be the result of preexisting differences in moss species and microflora (food resources).

In controlled fumigation experiments, moss-invertebrate associations can be exposed to different concentrations of a single pollutant. The comparison of the response of the fauna with a control receiving unpolluted air is used to quantify specific effects of pollution. In exposure experiments the effects of a complex mixture of air pollutants are simultaneously assessed. Therefore, these experiments are more realistic than fumigation experiments, but the risk to introduce artefacts (e.g. differences in microclimate) is higher under field conditions. The synthesis of both fumigation and exposure experiments, supplemented by findings of a natural survey (STEINER, 1994a, b, c, 1995) warrants optimal insight into effects of air pollution on moss-invertebrate associations.

2 MATERIAL AND METHODS

Fumigation and exposure experiments were performed with the fauna of tegulous (living on tiles; from Latin: "tegula" = tile) mosses collected from an intermediately polluted site in Zürich (site "F"; STEINER, 1994a). Nematodes and tardigrades were determined to the species level; rotifers were treated as a group. Methods for processing the fauna are outlined by STEINER (1994a). To minimise disturbance caused by repeated destructive sampling, the sample size was fixed empirically to one sampling unit of 1 cm²/cushion (= one sample). In the supplementary exposure experiments, two samples were taken per moss cushion. Four moss-grown tiles (= replicates) were exposed to each SO₂ concentration and at each exposure site. The small sample size was inappropriate for studying the temporal variation of microarthropod communities. Nevertheless, qualitative data are available providing information on the tolerance of some oribatid and collembolan species.

The nematodes *Geomonhystera australis* (Cobb) and *G. villosa* (Bütschli) are treated as a single taxon (i.e. *Geomonhystera* sp.), since it was not possible to separate their juveniles. The taxon Plectidae sp. is composed of predominantly first

larval instars. The tardigrade *Macrobiotus* sp. consists of individuals that couldn't be properly identified (tuns, moulting individuals, young individuals).

2.1 FUMIGATION EXPERIMENTS

The flat roofing tiles used in the fumigation experiments were fabricated yellow clay tiles (type 2), dominated by the moss species *Hypnum cupressiforme* (Hedw.) s.l. (with respect to percent cover). Other important species were *Schistidium apocarpum* (Hedw.), *Bryum capillare* Hedw. s.l. and *Tortula ruralis* Gärtn., Meyer & Scherb. (STEINER, 1994a). The size of the moss cushions ranged initially between 32 and 150 cm². In June 1982, four moss-covered tiles were placed into each of four closed Plexiglas fumigation chambers (diameter 2m, height 3m) with a 1.5-fold air change/min. A detailed description of the fumigation installation is given by KELLER (1976). Ambient air and three controlled levels of SO₂ were applied, resulting in the following treatments: 1) Control: unfiltered air of the rural-residential area of site "Bi" (see STEINER, 1994a), with a mean SO₂ concentration of 12 µg/m³ (~0.005 ppm) in 1983 (BLEULER & BUCHER, 1984); 2) 0.025 ppm (~65 µg/m³); 3) 0.075 ppm (~195 µg/m³); 4) 0.225 ppm (~585 µg/m³). The fumigation lasted 18 months until December 1983. During the whole period, the tiles were watered twice a week. The quality of the unfiltered air in the control chamber varied with time (e.g. SO₂: 45 µg/m³ in January 1983, 5 µg/m³ in August 1983; see BLEULER & BUCHER, 1984).

Two approaches were made for investigating the effects of SO₂ on moss-dwelling animals: a) investigation of treatment effects throughout the fumigation period, and b) assessment of the ultimate species composition at the end of the fumigation experiments. The initial species composition (June 1982) was assessed by taking one sampling unit from each of the six largest moss cushions. These samples were taken as follows: control = two samples; 0.025 ppm SO₂ = one; 0.075 ppm = one; 0.225 ppm = two. During the experiments, the faunal composition of each moss cushion was surveyed by taking one sample every three months. After the last sampling in December 1983, the remaining moss cushions were removed (after measuring their size) from the tiles. Extraction of the inhabiting fauna and measurement of the pH of the moss cushions were performed according to STEINER (1994b).

Median values of abundance of the four replicates per treatment were used to represent common trends in the response of the fauna to SO₂. Species richness was assessed by counting the number of species present in any of the four replicates/treatment (total number of species). The Kruskal-Wallis one-way analysis of variance by ranks was used to investigate statistical relationships between SO₂ concentrations and biotic (species richness, total abundance, abundance of selected taxa) or abiotic characteristics (pH, size and weight of moss cushions).

2.2 EXPOSURE EXPERIMENTS

Exposure experiments were conducted at 12 sites in the region of Zürich. Pollution ratings and abbreviations for exposure sites are given by STEINER (1994a).

Changes in faunal composition were related to NO_2 concentrations, since more nematode and tardigrade taxa were affected by NO_2 than by SO_2 (STEINER, 1994b). Furthermore, NO_2 can be considered representative of automotive emissions (GARNETT, 1979), which represent the main pollution source at roadside sites. The control site was identical with site "F", from where all the tiles originated. At each exposure site groups of four tiles were mounted on wooden bars (10 x 10 x 100 cm). The inclination and orientation of the tiles were identical to that of the roof from which they were collected. Microclimatic conditions, as well as the substrata supporting the tiles differed between exposure sites: unshaded metal sheets (sites "F", "D", "K" and "Tä"); unshaded concrete ("C"); partially shaded concrete ("Rä", "R" and "Ks"), boards ("T") and gravel ("Y" and "Z"); shaded asbestos sheets ("L").

The main exposure experiments were conducted between May 1982 and March 1985, using two types of flat roofing tiles. The tiles were collected from different parts of a north facing roof at site "F": relatively new red clay tiles (type 1), old and yellow clay tiles (type 2, as used in fumigation experiments). The dominant moss species of tile type 1 and 2 was *Ceratodon purpureus* (Hedw.) and *H. cupressiforme* s.l., respectively. Two tiles of each type were exposed at each exposure site. Sampling was performed at regular intervals of four months. Initial sampling occurred after an exposure period of four months (September 1982). At a given site sampling was carried out as long as the size of at least two moss cushions was large enough ($> 10 \text{ cm}^2$). Then, five samples were taken to assess the ultimate species composition.

Supplementary exposure experiments were performed at exposure sites where either the moss cushions had disappeared (sites "K", "L", "Tä"), or the inhabiting fauna became extinct after a short exposure period ("F", "R", "Rä"). Yellow clay tiles (types 3 and 4) collected in April 1983 from both sides of a second roof at site "F" were used, referring to different roof sides. Because the roof was shaded all day by a group of trees, the flora of tile types 3 and 4 was very similar (STEINER, 1990). Four tiles were exposed at each site (two tiles of each type). At the sites "R" and "Tä", only the missing moss cushions (two and one, respectively) were replaced. Sampling started in September 1983 (initial sampling) and was performed at regular intervals of four months. The ultimate species composition was defined by taking five samples from each cushion in September 1984.

3 RESULTS AND DISCUSSION

In the fumigation experiments, a total of 3'927 rotifers, 11'135 nematodes, 24'896 tardigrades, 329 mites, 599 springtails and one dipteran was found. Even more individuals were recorded in the exposure experiments (i.e. 25'869 rotifers, 27'426 nematodes, 58'716 tardigrades, 658 mites, 595 springtails and 39 other arthropods). Detailed information on the overall species composition is given by STEINER (1994a).

3.1 FUMIGATION EXPERIMENTS

3.1.1 *Treatment effects throughout the fumigation period*

Faunal composition of the moss cushions prior to fumigation was very similar (STEINER, 1990). Among the 194 nematodes initially recorded, the predominant

species were *Chiloplectus* cf. *andrassyi* (Timm) (relative abundance: 49%), *Paratripyla intermedia* (Bütschli) (23%) and *Prionchulus muscorum* (Dujardin) (5%). Tardigrades were represented by 171 individuals belonging to the Heterotardigrada (15%) and the Eutardigrada (85%). *Macrobiotus areolatus* Murray was the dominant tardigrade species (37%) followed by *M.* cf. *artipharyngis* Iharos (28%), *Echiniscus blumi* Richters (15%) and *M. hufelandi* Schultze (6%).

TOTAL NEMATODES AND TARDIGRADES

Treatment effects on the abundance of nematodes and tardigrades are shown in fig. 1. The percentage of nematodes in the four treatments was approximately identical after a fumigation period of three months (September 1982). Decline of nematode populations became obvious between December 1982 and March 1983 (fig. 1A). In particular, the abundance of nematodes was strongly reduced in the chamber with the highest SO_2 concentration. Until December 1983, fumigation with 0.225 ppm SO_2 led to a constant reduction in nematodes. The two other treatments had little influence on total nematode numbers for 15 months. Thereon, nematode populations declined as compared with the control.

Tardigrades were adversely affected by the highest SO_2 treatment from the beginning (fig. 1B). The relative abundance of tardigrades in the other treatments varied only slightly, except for the relative increase between June and September

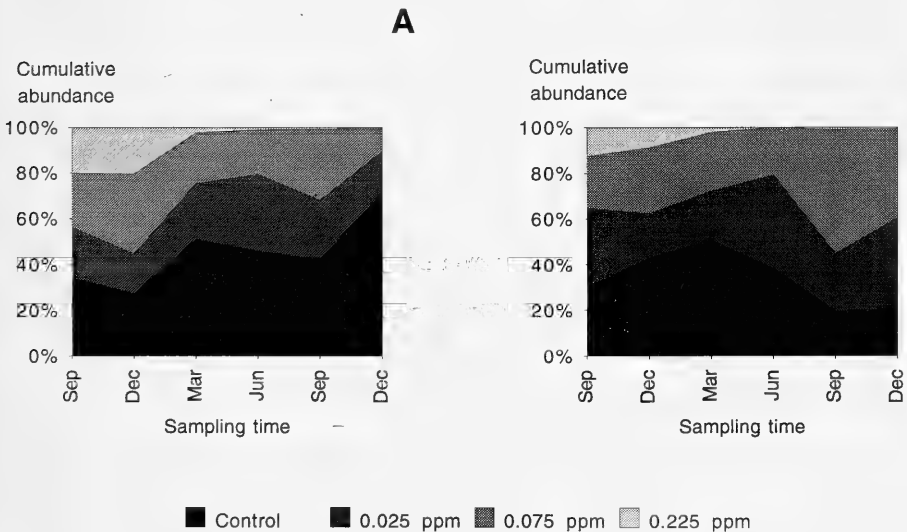


FIG. 1

Temporal variation in percent nematode (A) and tardigrade (B) representation at different SO_2 concentrations (abundance: median; sampling period: September 1982 to December 1983).

TAB. 1.

Variation [standard error of median/median; in %] of rotifer, nematode and tardigrade numbers within the sampling units of each treatment. Variation coefficients are given for the first sampling and for total counts (A: control = 0.005 ppm; B: 0.025 ppm; C: 0.075 ppm; D: 0.225 ppm SO₂; -: median was zero).

Taxa	Treatments	Variation coefficients							
		First sampling				Total counts			
		A	B	C	D	A	B	C	D
Rotifers		132	46	18	44	11	42	43	414
Nematodes		31	45	19	35	30	49	87	180
<i>Aphelenchoides</i> sp.		-	-	-	-	148	82	-	-
<i>Plectidae</i> sp.		58	173	58	58	28	98	126	-
<i>Plectus acuminatus</i> s.l.		115	-	77	-	85	46	16	93
<i>Plectus</i> cf. <i>parietinus</i>		-	-	-	-	-	-	33	-
<i>Chiloplectus</i> cf. <i>andrassyi</i>		34	55	33	35	31	47	99	-
<i>Paratripyla intermedia</i>		38	26	14	38	212	-	183	-
<i>Prionchulus muscorum</i>		58	173	19	-	-	72	-	-
Tardigrades		21	22	55	150	14	24	32	>1000
<i>Macrobiotus areolatus</i>		24	50	102	96	18	47	55	>1000
<i>Macrobiotus hufelandi</i>		27	113	34	229	21	45	38	914
<i>Macrobiotus</i> cf. <i>artipharyngis</i>		22	29	58	231	32	93	112	-
<i>Milnesium tardigradum</i>		-	-	-	-	-	-	129	-
<i>Echiniscus blumi</i>		115	86	107	89	74	86	62	>1000
<i>Echiniscus testudo</i>		-	-	-	-	40	919	313	-

1983 in the 0.075 ppm treatment. Note that the variation in tardigrade numbers was relatively large in the replicates of the two highest treatments (tab. 1).

ABUNDANCES OF SPECIES

At the first sampling of all the 16 moss cushions (September 1982), fumigation with SO₂ showed no adverse effects, except on *P. intermedia* (tab. 2). Although initial counts of *P. intermedia* (June 1982) in those moss cushions designated for the highest treatment revealed average densities, its abundance at the first sampling was significantly smaller than in the other treatments.

The temporal variation in species specific nematode and tardigrade populations is represented for each treatment in figs. 2 and 3, respectively. Since the variation of abundance estimates was sometimes relatively high (tab. 1), temporal fluctuations in population sizes (especially of rare species and in the highest treatment) are not necessarily significant. However, there was a general trend of population reduction after a fumigation period of 12 to 18 months. This could be caused by the transplantation of the moss cushions from their natural habitat into fumigation chambers with less favourable environmental conditions.

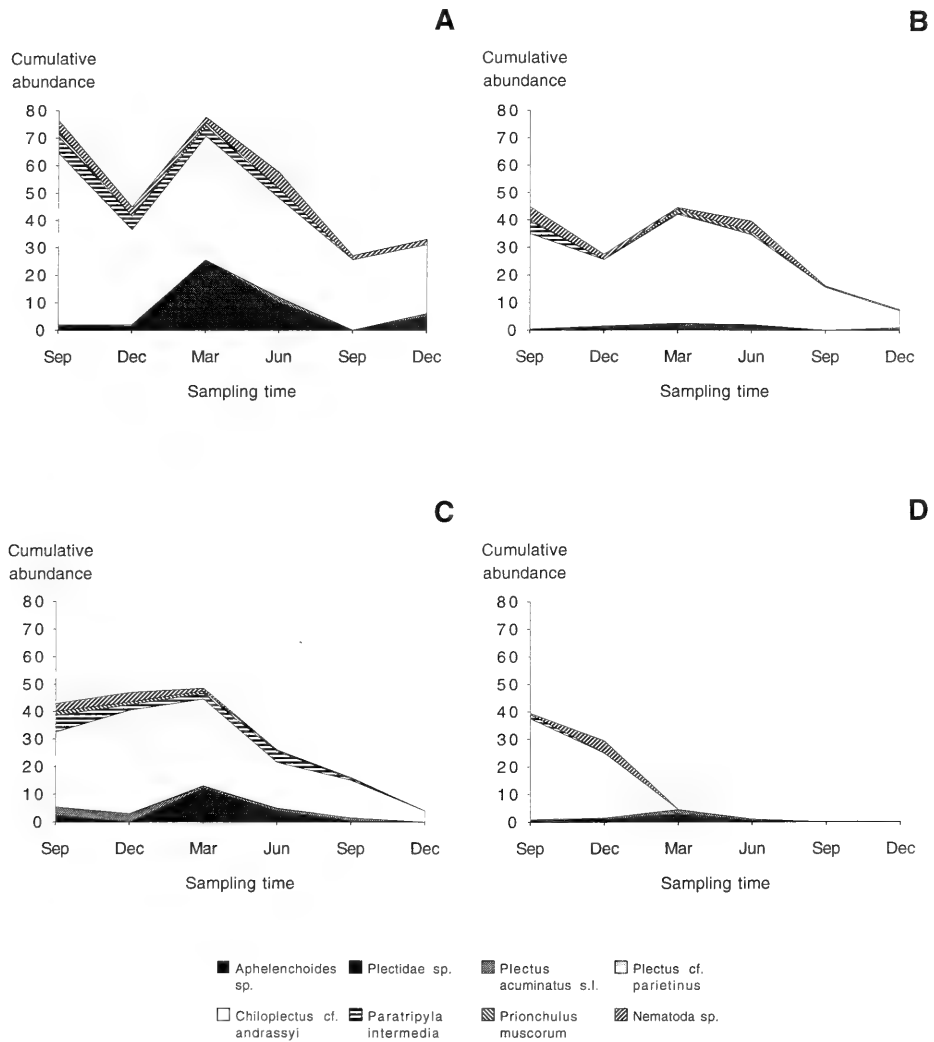


FIG. 2

Variation in species specific nematode populations (individuals/cm²; median) at different SO₂ concentrations (A: control = 0.005 ppm; B: 0.025 ppm; C: 0.075 ppm; D: 0.225 ppm; sampling period: September 1982 to December 1983; Nematoda sp.: unidentified individuals).

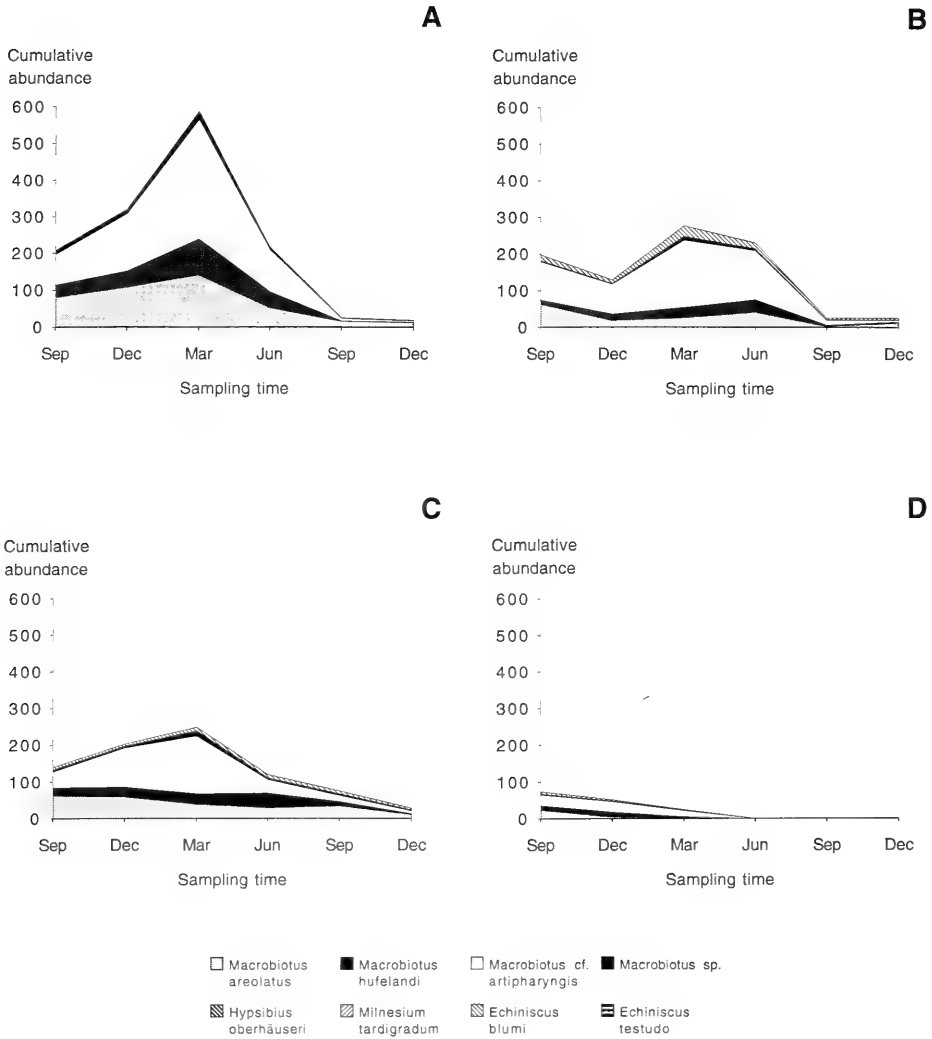


FIG. 3

Variation in species specific tardigrade populations (individuals/cm²; median) at different SO₂ concentrations (A: control = 0.005 ppm; B: 0.025 ppm; C: 0.075 ppm; D: 0.225 ppm; sampling period: September 1982 to December 1983).

Population peaks of nematodes were evident in September 1982 and March 1983, mainly due to the high abundance of *C. cf. andrassyi*. This species was present in all treatments at almost all the sampling dates. *Chiloplectus cf. andrassyi*, a potential indicator species of air pollution (STEINER, 1994b), disappeared in the highest treatment between December 1982 and March 1983 (fig. 2D). From March 1983 onwards the abundance of *C. cf. andrassyi* decreased constantly in the treatments with 0.025 and 0.075 ppm SO₂, but remained stable in the control. The reduction in abundance of this bacterial-feeding nematode could be a consequence of reduced bacterial growth due to acidification in the fumigated moss cushions. Only *Plectus acuminatus* Bastian s.l. survived fumigation with 0.225 ppm SO₂ until the end of the experiment, while small populations of *Aphelenchoides* sp. and *P. muscorum* persisted until June and September 1983, respectively. This is in contrast to results obtained by LEETHAM *et al.* (1982), showing that both stylet bearing nematodes and Mononchida appeared unaffected by fumigation with SO₂. The number of *P. intermedia* – a potential indicator species (STEINER, 1994b) – decreased from the beginning at the highest concentration (tab. 2), but declined also in the other treatments. Other species were too rare to analyse their response to SO₂.

The dynamics of tardigrade populations (fig. 3) were very similar to that of nematodes, except for the single peak in the control. Again, annual population fluctuations were most pronounced in the control. Populations reached a peak in March 1983 (fig. 3A-C). This indicates favourable conditions at least over a period of nine months (June 1982 to March 1983). Thereon, tardigrades became rare irrespective of the SO₂ concentration. In contrast, LEETHAM *et al.* (1982) found a substantial reduction in tardigrade numbers in field plots fumigated with ca 0.025 to 0.075 ppm SO₂, when compared with the control (ca 0.008 ppm). Since species identification was lacking, this contradictory response of tardigrades remains unexplained.

The species composition at the first sampling occasion revealed no significant differences among treatments (tab. 2). The dominant species *M. cf. artipharyngis*, *M. areolatus* and *M. hufelandi* were present in all treatments and on almost all the sampling dates. At the highest SO₂ concentration, populations of the three species were reduced from the beginning and reached a median of zero in June 1983 (fig. 3D). However, small populations of these species were found by analysing the entire moss cushions (fig. 6B). The heterotardigrade species *E. blumi* was more resistant to SO₂ pollution than the *Macrobiotus* species. *Echiniscus blumi* is the only species typically encountered (median > 0) throughout the study at the highest SO₂ concentration. Surprisingly, the abundance of *E. blumi* was similar in the control and in the 0.225 ppm treatment at all sampling dates. Other tardigrade species were too rare, and the accuracy of population estimates too low (tab. 1) to indicate their sensitivity to SO₂ pollution.

SPECIES RICHNESS OF NEMATODES

Throughout the fumigation experiments, moss cushions from the 0.225 ppm SO₂ treatment were characterised by the lowest species richness (fig. 4A). The

TAB. 2

Abundance of species (individuals/cm²), community characteristics and abiotic factors for which the Kruskal-Wallis test showed significant differences among treatments ($P < 0.05$). The analysis is based on the first sampling (September 1982), and on total counts (December 1983) (TA: tardigrades; NE: nematodes; Ranks: arrangement of treatments according to their ranks; A: control = 0.005 ppm; B: 0.025 ppm; C: 0.075 ppm; D: 0.225 ppm SO₂; P: probability of the Kruskal-Wallis test, corrected for ties).

Variables	Ranks				P
First sampling					
NE: <i>Paratripyla intermedia</i>	C ~	A >	B >	D	0.028
Total counts					
NE: <i>Chiloplectus</i> cf. <i>andrassyi</i>	A >	B >	C >	D	0.009
Nematodes (abundance)	A >	B >	C >	D	0.008
Nematodes (species number)	A ~	B ~	C >	D	0.036
TA: <i>Macrobiotus hufelandi</i>	B =	C >	A >	D	0.007
<i>Macrobiotus</i> cf. <i>artipharyngis</i>	B >	C >	A >	D	0.009
<i>Echiniscus blumi</i>	C ~	B >	A >	D	0.008
Eutardigrades (abundance)	C ~	B >	A >	D	0.024
Heterotardigrades (abundance)	B =	C >	A >	D	0.006
Tardigrades (species number)	B >	C ~	A >	D	0.032
Abiotic factors					
pH of moss cushions	A >	B >	C >	D	0.003

number of species declined in this treatment after a fumigation period of three to six months, which parallels the reduction in nematode abundance (fig. 2D). Surprisingly, though, species richness reached approximately the same levels in the control as in the intermediate treatments (fig. 4A). Irrespective of the SO₂ concentration, there was a general trend for a reduction in species number between June and September 1983. This could be due to the high temperatures in July 1983, the hottest month in the century (mean temperature 22°C).

SPECIES RICHNESS OF TARDIGRADES

Maximum species richness was found in the treatments with 0.025 (December 1982 and March 1983) and 0.225 ppm SO₂ (March 1983). The number of species was considerably stable throughout the fumigation period (fig. 4B), although the abundance of tardigrades decreased from March 1983 onwards (fig. 3). As already noted for nematodes, the number of species at the end of the fumigation period was lowest in moss cushions from the highest treatment. Differences between the other treatments were usually small (fig. 4B). Due to the relatively small samples, some rare species escaped detection at the end of the fumigation experiments (e.g. *M. areolatus* and *M. hufelandi* in the 0.225 ppm treatment; see fig. 6B).

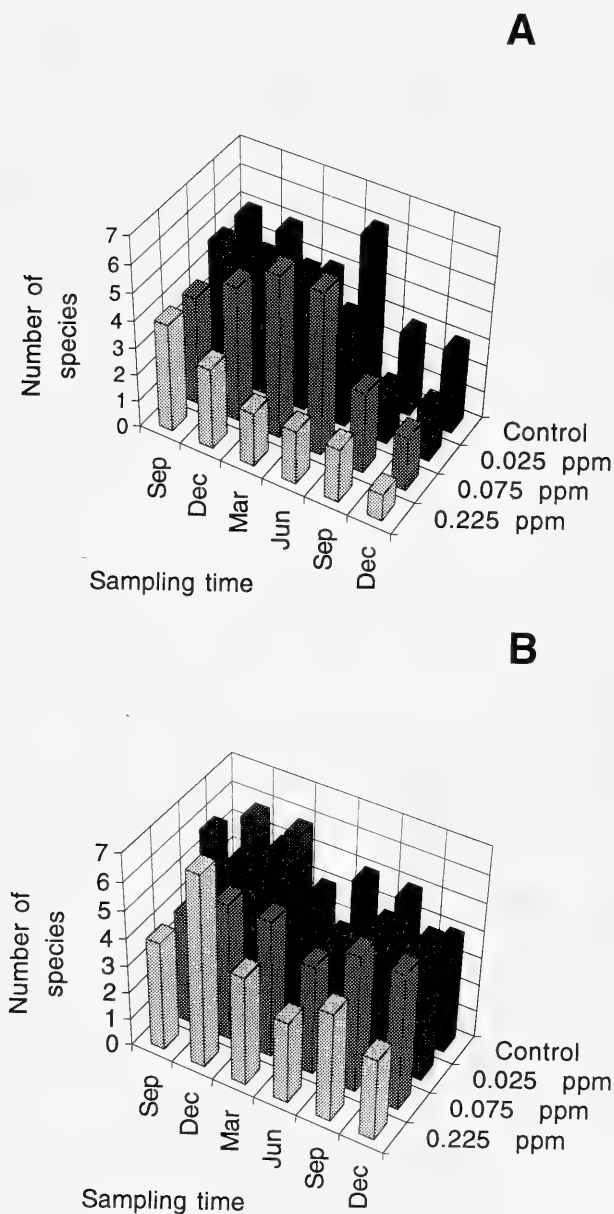


FIG. 4

Temporal variation in species richness (total number of species) of nematodes (A) and tardigrades (B) at different SO_2 concentrations (sampling period: September 1982 to December 1983).

ROTIFERS AND ARTHROPODS

The response of rotifers to SO_2 was similar to that of nematodes. After nine months, rotifer numbers (median of four replicates) were highest in the control and lowest in the 0.225 ppm SO_2 treatment. The abundance of rotifers in the two intermediate treatments was approximately of the same size throughout the experiment. In contrast, LEETHAM *et al.* (1982) noted in field plots fumigated with ca 0.075 ppm SO_2 slight but consistent trends of reduction in rotifer numbers.

The dominant arthropod species were the collembolan species *Xenylla brevisimilis* Stach (overall abundance: 458 individuals), as well as the oribatid mites *Trhypochthonius tectorum* Berlese (84) and *Scutovertex* cf. *sculptus* Michaël (32). Other arthropod taxa encountered are listed by STEINER (1994a). Only a few species survived the 0.225 ppm (i.e. *T. tectorum*) and the 0.075 ppm SO_2 treatments (i.e. *S.* cf. *sculptus* and *X. brevisimilis*). In the control, the three former species were found together with *Tectocephus sarekensis* Trägårdh.

3.1.2 Ultimate composition

Fig. 5 shows for each SO_2 treatment the abundance of rotifers, nematodes, eutardigrades and heterotardigrades at the end of the fumigation experiments. Fumigation with 0.225 ppm SO_2 strongly reduced the abundances of all the taxa

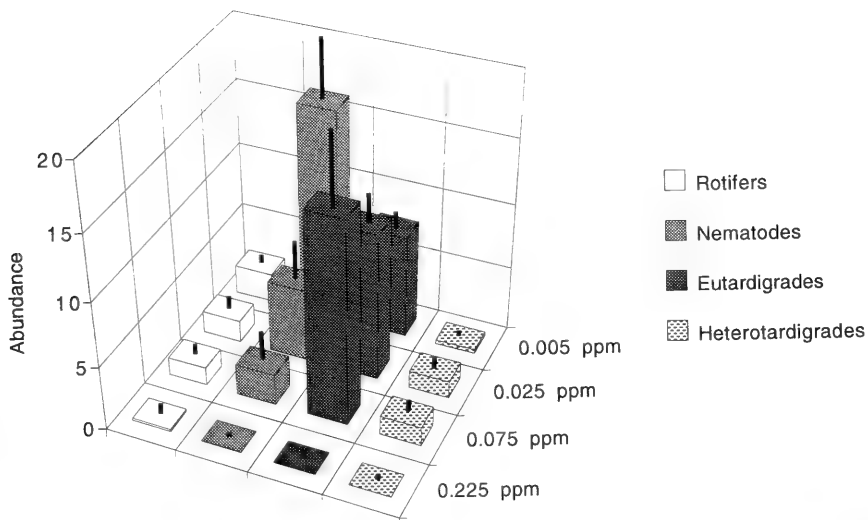


FIG. 5

Abundance (individuals/cm²; median + standard error of median) of rotifers, nematodes, eutardigrades and heterotardigrades in the SO_2 treatments after a fumigation period of 18 months (December 1983).

under consideration. The abundance of nematodes and tardigrade varied significantly with SO_2 concentrations (tab. 2), but differed in their response patterns. While nematode numbers showed a consistent decrease with increasing pollution, eutardigrades and heterotardigrades reached largest populations in the treatments with low and intermediate concentrations. The potential of tardigrades to endure extreme environmental conditions, such as the hot summer of 1983, in a state of anhydrobiosis (RAHM, 1923; CROWE, 1975) could render them more resistant to SO_2 than the nematodes. The observed response of tardigrades to SO_2 is in clear contrast to findings by LEETHAM *et al.* (1982), who found that even a concentration of 0.025 ppm SO_2 had a negative influence on the tardigrade numbers. The response of rotifers to SO_2 pollution was similar to that of nematodes.

NEMATODES

A total of 6'937 nematodes (9 species) was extracted at the end of the fumigation experiments. *Chiloplectus* cf. *andrassyi* (relative abundance: 80%) clearly dominated the nematode community. *Aphelenchoides* sp. 5 (6%), *Plectus acuminatus* s.l. (3%) and *Paratripyla intermedia* (3%) were the most important accompanying species. Large nematode populations were realised in the control and in the fumigation experiment with the lowest SO_2 concentration (fig. 6A). Only for *C.* cf. *andrassyi* a significant reduction in population density with increasing fumigation concentration (tab. 2) was found. However, the variation of population estimates was usually high (tab. 1). *Plectus* cf. *parietinus* Bastian and *Prionchulus muscorum* were most frequent (median > 0) in the intermediate treatments. *Plectus acuminatus* s.l. was the only nematode species with a median > 0 at the highest concentration. Nematode species not included in fig. 6A were exceedingly rare (i.e. *Panagrolaimus* cf. *rigidus* [Schneider], *Plectus parvus* Bastian and *Ypsilonellus* sp.).

TARDIGRADES

A total of 9'214 tardigrades (8 species) was found in the 16 moss cushions at the end of the fumigation experiments. They were represented by the classes Heterotardigrada (relative abundance: 12%) and Eutardigrada (88%). *Macrobiotus areolatus* (52%), *M.* cf. *artipharyngis* (21%), *M. hufelandi* (12%) and *Echiniscus blumi* (11%) were the dominant species (fig. 6B). These species (except *M. areolatus*) reached highest densities in the treatments with 0.025 and 0.075 ppm SO_2 (tab. 2). This suggests that the tardigrades responded to other factors than the nematodes (fig. 6A). *Echiniscus blumi*, *M. areolatus*, *M. hufelandi* and *M. artipharyngis* were the only tardigrade species surviving the 0.225 ppm treatment, but only the former three species reached a median > 0 (fig. 6B). Tardigrade species not included in fig. 6B were found in very low numbers (i.e. *Macrobiotus persimilis* Binda & Pilato, *Hypsibius convergens* [Urbanowicz] s.l. and *H. oberhaeuseri* Doyère).

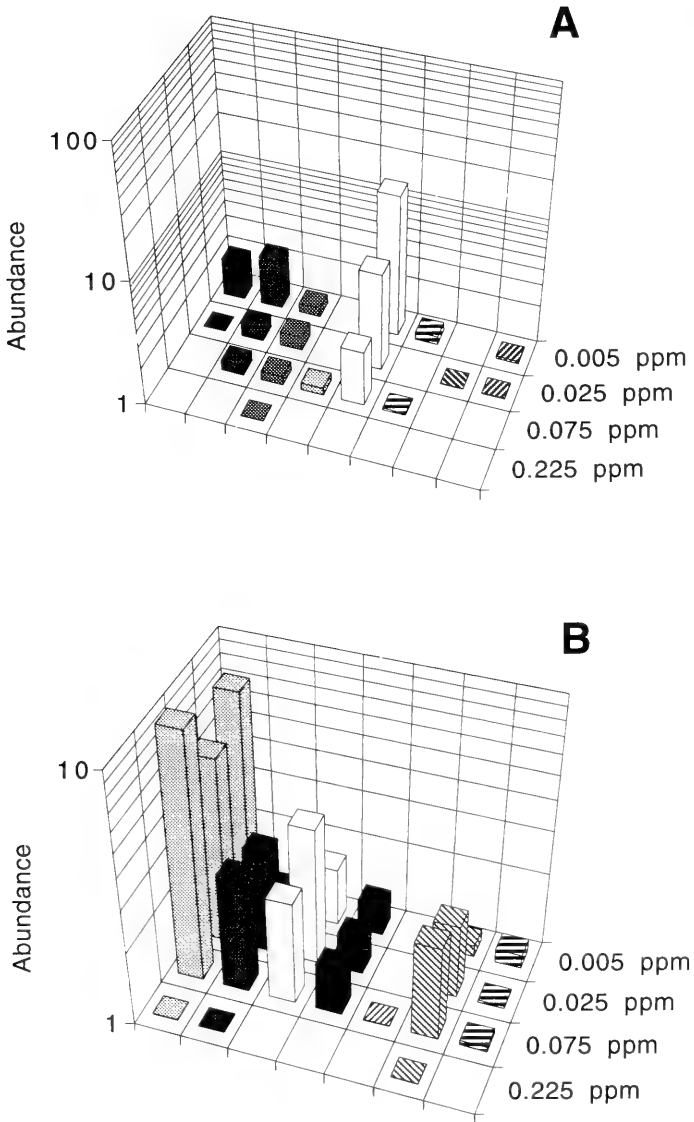


FIG. 6

Nematode (A) and tardigrade (B) species representation (individuals/cm²; median) in the SO₂ treatments after a fumigation period of 18 months (December 1983). For graphical patterns see figs 2 and 3.

ARTHROPODS

Xenylla brevisimilis (125 individuals), *Trhypochthonius tectorum* (121) and *Scutovertex* cf. *sculptus* (62) dominated numerically. The latter two oribatid species, along with the springtail *Folsomia angularis* Axelson, were the only arthropods extracted from moss cushions exposed to 0.225 ppm SO₂. The density of *X. brevisimilis* decreased with increasing SO₂ concentrations and no individuals were found in the highest treatment. This collembolan species could be an indicator of high levels of SO₂ pollution (i.e. > 0.075 ppm).

CHANGES OF THE FUMIGATED MOSS CUSHIONS

First visible signs of injury (bleaching of leaves) were noted for the moss cushions treated with 0.225 ppm SO₂ after 12 months of fumigation (June 1983). Thereon, the leaves of these cushions changed from green to golden-brown (loss of chlorophyll) and they were covered at the apex with white crystals. In the other treatments, no visible changes were found that could be related to SO₂ concentrations. However, the pH of the 16 fumigated moss cushions decreased significantly with increasing SO₂ concentrations (tab. 2, fig. 7). Normal pH conditions as represented by the control (= 0.005 ppm SO₂) ranged between 7.4 and 8.2. This is within the typical pH range of older tiles (VON DER DUNK, 1988a). Fumigation with 0.225 ppm SO₂ decreased moss pH by approximately 3 units in comparison with the control (fig. 7).

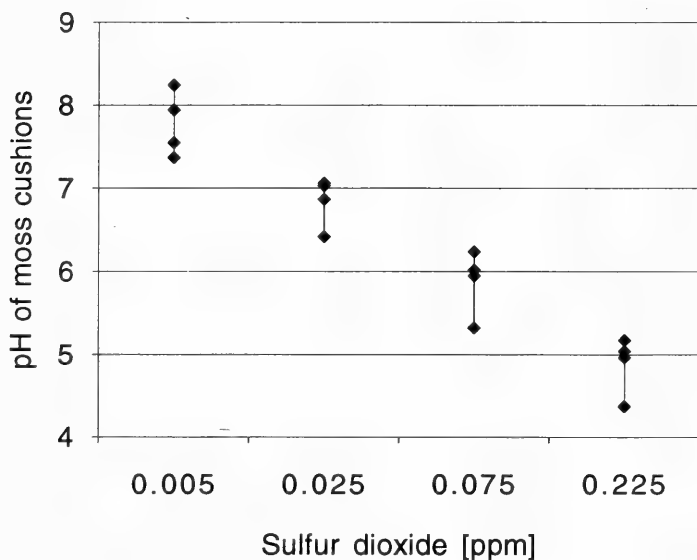


FIG. 7

The pH values of the moss cushions in the SO₂ treatments after a fumigation period of 18 months (December 1983).

Since bacteria usually have a pH optimum near neutrality, whereas most fungi are associated with acid conditions (CLARK, 1967; SMITH & WALTON, 1985), it is likely that the aquatic fauna responded to changes in microflora suitability and availability. Soil acidification therefore decreases bacterial numbers and/or microbial activity (PERSSON *et al.*, 1989; SUTTON *et al.*, 1991; RUESS & FUNKE, 1992). As a consequence, the decline in nematode species following acidification is usually observed within the bacterial feeders (PERSSON *et al.*, 1989; RUESS & FUNKE, 1992). Changes of pH values also have documented effects on the survival and the reproduction ability of plant parasitic nematodes (MORGAN & MACLEAN, 1968; BRZESKI & DOWE, 1969). Hatching of these nematodes was strongly inhibited at pH 4 and reached a maximum near neutrality. Additionally, a possible mechanism by which pH influences the aquatic fauna is through toxicity of heavy metals. Heavy metals have been reported to accumulate in mosses (LITTLE & MARTIN, 1974; RASMUSSEN, 1977). The lower the pH, the less is sorption of metals to organic matter. BENGTSSON *et al.* (1986) pointed out that metals caused a significant reduction in both abundance and diversity of soil invertebrates. The final effect of pH could also be strongly modified by its interaction with SO₂ as discussed below.

CHEMISTRY OF SO₂

The form in which SO₂ enters the fumigation chamber is not the same as it actually impacts the aquatic fauna. Since the moss-dwelling aquatic fauna is only active when the moss cushion is permeated with water, toxic effects of SO₂ are likely to operate through the aqueous phase. The predominant chemical reactions of SO₂ depend on humidity conditions (BABICH & STOTZKY, 1974). The moist moss cushion will rapidly absorb gaseous SO₂ into water causing acidification. The components present in the aqueous phase beside dissolved SO₂ include sulfurous acid (H₂SO₃), bisulfite (HSO₃⁻), sulfite (SO₃²⁻) and sulfate (SO₄²⁻). Between pH 1.8 and 7.2, bisulfite is dominant, while above pH 7.2 sulfite predominates. BABICH & STOTZKY (1974) list percentages of the major forms of SO₂ in water dependent on prevailing pH conditions.

Species richness of soil-dwelling nematodes was strongly reduced by the contamination of the soil surface with H₂SO₄ (RATAJCZAK *et al.*, 1989; RUESS *et al.*, 1993). However, direct toxic effects of sulfur compounds on nematodes, as well as the influence of acid deposition on nematodes is poorly described (SHAFFER *et al.*, 1992). It seems that indirect effects of the different forms of SO₂ on nematode food resources must be considered to account for the impact on nematodes. Especially bisulfite is toxic to sensitive moss species and to all protonema of mosses (GILBERT, 1968). BABICH & STOTZKY (1974) showed that bisulfite had an inhibitory effect also on bacteria, which increased with decreasing pH values. In fact, gaseous SO₂ and formation products inhibit microbial activity (GRANT *et al.*, 1979) and primary production at the microbial level (BABICH & STOTZKY, 1974). The sharp decrease in nematode populations (especially of *C. cf. andrassyi*) in the highest treatment (fig.

2D) could therefore be a consequence of increasing concentrations of bisulfite, due to continually decreasing pH values during SO₂ fumigation.

The mechanism by which tardigrades are affected by SO₂ is not known (LEETHAM *et al.*, 1982). Their feeding habits are hardly known. It is thus unclear if tardigrade populations were impacted by similar reductions of their major food sources (bacteria, fungi, algae, protozoans, rotifers and/or nematodes), or by direct toxicity of SO₂ and formation products.

3.2 EXPOSURE EXPERIMENTS

The influence of exposure on the moss-dwelling fauna is mainly discussed with respect to species survival (i.e. comparison of initial and ultimate species composition), since the assessment of a species' presence requires relatively few replicates and is not bound to a certain season (STEINER, 1994c).

3.2.1 Initial species composition

MAIN EXPOSURE SERIES

The composition of the aquatic fauna at the first sampling (after an exposure period of four months) is indicated in fig. 8. A total of 1139 nematodes (nine species), 1742 tardigrades (eight species) and 1720 rotifers was encountered (tile type 1: 20 samples; type 2: 19). The sites "Rä" and "F" are disregarded in the characterisation of the initial species composition, since their fauna had already been considerably reduced at the first sampling (fig. 8).

The fauna of tile type 1 and tile type 2 moss cushions differed slightly. By exposing two tiles of each type at any site, the faunal differences among tile types were irrelevant for intersite comparison. The dominant nematode species were *Chiloplectus* cf. *andrassyi* (relative abundance in tile type 1: 47%; type 2: 64%) and *Paratripyla intermedia* (19 and 26%). In addition, *Prionchulus muscorum* was abundant (18%) in mosses of type 1. *Echiniscus blumi* was the dominant tardigrade species in mosses of tile type 1 (60%) followed by *Macrobiotus hufelandi* (19%) and *M. cf. artipharyngis* (16%). Mosses of tile type 2 were dominated by *M. cf. artipharyngis* (32%), *M. areolatus* (31%) and *M. hufelandi* (25%).

The density of rotifers (median) in the samples from tile type 1 was approximately two-thirds of that from tile type 2 (30 individuals/cm²), a similar ratio as already noted for nematodes. Moss-dwelling arthropods were generally rare (each taxa ≤ 8). The following taxa were found (in decreasing abundance): *Xenylla brevisimilis*, *Scutovertex* cf. *sculptus*, *Trhypochthonius tectorum*, *Phauloppia lucorum* (Koch), *Scheloribates latipes* (Koch), dipteran larvae, *Tectocephus sarekensis*, *Trichoribates* cf. *trimaculatus* (Koch), *Zygoribatula frisiae* (Oudemans), *Z. propinquus* (Oudemans), *Spinibdellinae* sp., *Sminthurinus* sp. and *Folsomides angularis*.

The fauna used in the main exposure series thus corresponds well to the fauna used in the simultaneously performed fumigation experiments (chapter 3.1). This is

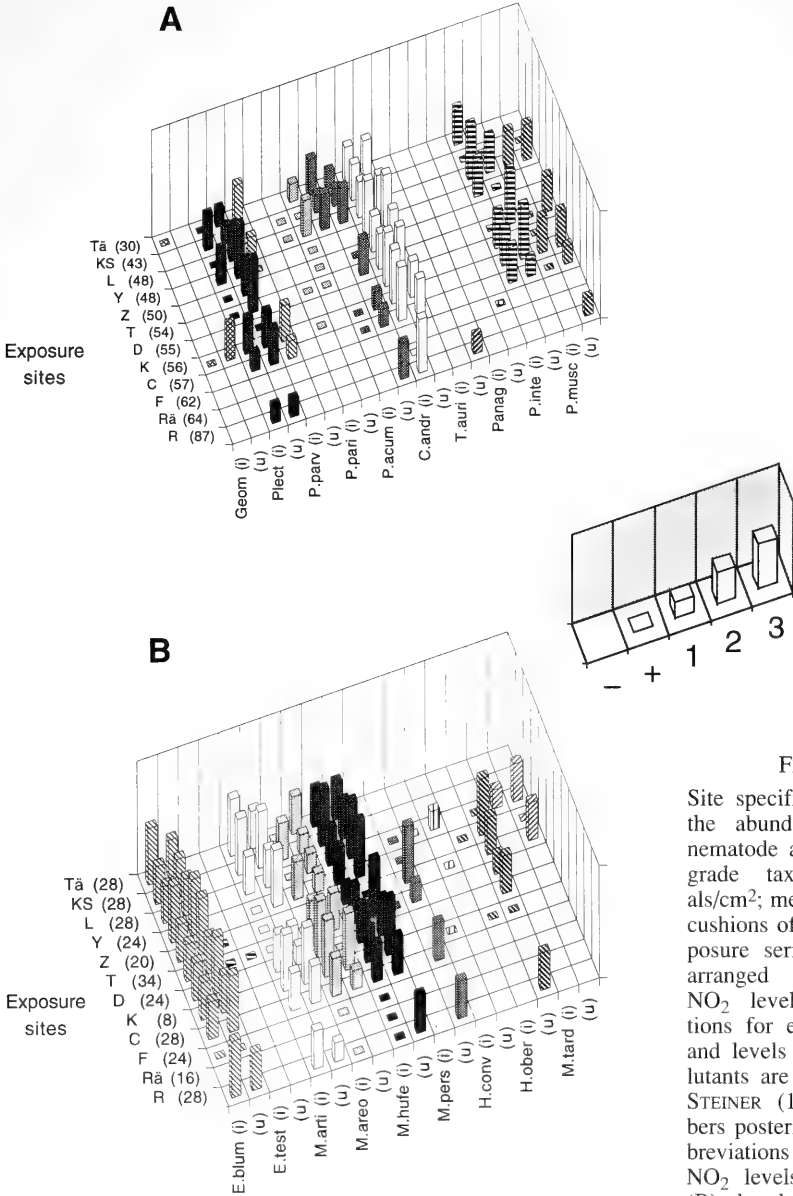


FIG. 8

Site specific changes in the abundance of (A) nematode and (B) tardigrade taxa (individuals/cm²; median) in moss cushions of the main exposure series. Sites are arranged according to NO₂ levels. Abbreviations for exposure sites and levels of other pollutants are explained by STEINER (1994a). Numbers posterior to site abbreviations denote in (A) NO₂ levels (µg/m³), in (B) the duration of the

exposure period (in months). (i) = initial composition; (u) = ultimate composition; abundance values: -) absent; +) present, but median = 0; 1) 0 < median < 1; 2) 1 < median < 10; 3) median ≥ 10. Abbreviations for taxa (in alphabetic order): C.andr: *Chiloplectus* cf. *andrassyi*; E.blum: *Echiniscus blumi*; E.test: *Echiniscus testudo*; Geom: *Geomonhystera* sp.; H.conv: *Hypsibius convergens* s.l.; H.ober: *Hypsibius oberhaeuseri*; M.areo: *Macrobiotus areolatus*; M.arti: *Macrobiotus* cf. *artipharyngis*; M.hufe: *Macrobiotus hufelandi*; M.pers: *Macrobiotus persimilis*; M.tard: *Milnesium tardigradum*; P.acum: *Plectus acuminatus* s.l.; Panag: *Panagrolaimus* sp.; P.inte: *Paratrypila intermedia*; Plect: *Plectidae* sp.; P.musc: *Prionchulus muscorum*; P.pari: *Plectus* cf. *parietinus*; P.parv: *Plectus parvus*; T.auri: *Tylocephalus auriculatus*.

taken as evidence that there were no relevant faunal changes within the first exposure period of four months.

SUPPLEMENTARY EXPOSURE SERIES

Initial sampling revealed 1'299 nematodes (ten taxa) and 1'477 tardigrades (eight species). Dominant nematodes were *P. acuminatus* s.l. (25%), *Tylocephalus auriculatus* (Bütschli) (24%), unidentified Plectidae spp. (23%) and *Plectus parvus* (16%). *Hypsibius convergens* s.l. was the dominant tardigrade species (32%), with *M. areolatus* (29%), *H. oberhaeuseri* (18%) and *M. hufelandi* (15%) as the most abundant associated species. The abundance of nematode and tardigrade taxa is given for each exposure site in fig. 10.

As compared with the main exposure series, the dominance of unique nematode species is less expressed and qualitatively different in the supplementary experiment. *Panagrolaimus* cf. *rigidus*, *T. auriculatus*, *Aphelenchoides* sp., *Diphascopis pingue* (Marcus) and *Isohypsibius prosostomus* (Thulin) were found exclusively in moss cushions of the supplementary exposure series. On the other hand, several species found in the main exposure series were absent (i.e. *Echiniscus testudo* (Doyère), *Milnesium tardigradum* Doyère and *M. persimilis*) or exceedingly rare (i.e. *C. cf. andrassyi* and Tylenchidae sp.) in the supplementary study.

Rotifers reached the same density (median) as already found in mosses of tile type 2. Arthropods were represented by *T. sarekensis* (15 individuals), *S. cf. sculptus* (8), *X. brevisimilis* (4) and *Camisia segnis* (Hermann) (1). All species but *C. segnis* were also present in tegulous mosses of tile type 1 and/or 2.

3.2.2 Ultimate species composition

The actual species composing the community at the end of the exposure period (fig. 8) depend on a species initial presence, on its tolerance towards pollution and microclimatic conditions, as well as on its capacity for immigration or reimmigration from the surroundings. Faunal response to changes in environmental conditions can result from direct effects or from the response of the microflora forming the food source of the fauna. For example, the dependence of nematodes on soil moisture conditions was found to act through the density of microorganisms (SOHLENIUS & WASILEWSKA, 1984). Moreover, the microfloral composition is dependent on air pollution levels (BEWLEY & PARKINSON, 1986; KHANNA, 1986) and on the nutrient environment within the moss cushion that changes in accordance with dry and wet deposition of pollutants. Since the uptake of heavy metals differs between bacterial species (DOYLE *et al.*, 1975; DOELMAN *et al.*, 1984), invertebrates specialised on a specific bacterial flora are differently affected.

Whether the moss-invertebrate associations are negatively or positively affected depends on the interacting net effect of the simultaneously changing environmental conditions. Subsequently, an attempt is made to differentiate the effects of air pollution and microclimatic conditions.

EFFECTS OF AIR POLLUTION

In fig. 8, the exposure sites are arranged along a gradient of pollution. At relatively low levels of pollution, the moss-invertebrate associations were not significantly influenced by air quality. On the one hand almost all nematode and tardigrade species survived (sites "L" and "T"), while on the other most species initially encountered were strongly reduced (sites "Rä" and "F").

Chiloplectus cf. *andrassyi*, *Paratripyla intermedia* and *Macrobiotus areolatus* disappeared at the most polluted sites "R", "Rä" and "F" (fig. 8). However, faunal changes at the sites "Rä" and "F" have to be interpreted with care. Their fauna had already been strongly reduced until the first sampling (fig. 8). As the response of the moss-dwelling fauna to sustained and high concentrations of SO₂ was relatively slow (figs. 2D and 3D), the rapid changes observed at the sites "Rä" and "F" were probably caused by factors other than gaseous air pollutants. The sensitivity of *C. cf. andrassyi* to air pollution is corroborated by results of accompanying studies. Its abundance decreased significantly with increasing air pollution (STEINER, 1994b) and SO₂ concentrations in the fumigation experiments (tab. 2). The supposed sensitivity of *P. intermedia* to pollution is confirmed only by findings of the faunistic survey (STEINER, 1994b), while its response to SO₂ fumigation was inconclusive (chapter 3.1). Results for *M. areolatus* were inconsistent. In the faunistic survey (STEINER, 1994b) *M. areolatus* was restricted to rural moss cushions, but fumigation with SO₂ showed that this species can survive (in small populations) sustained high levels of pollution (fig. 6B).

In contrast to *C. cf. andrassyi*, *Macrobiotus persimilis* reached larger population levels at the more polluted sites (fig. 8B). *M. persimilis* – absent at the first sampling occasion in all sites but "T" – invaded moss cushions with native populations of *M. hufelandi* at several urban sites. This confirms that *M. persimilis* is better adapted to pollution than *M. hufelandi*, as already noted in the faunistic survey (STEINER, 1994b). The failure of *M. persimilis* to invade the exposed moss cushions at site "K" may be a result of the short exposure period, while the absence of *M. persimilis* at the rural site "D" confirms its low frequency at rural sites (STEINER, 1994b). *Plectus acuminatus* s.l. also tolerated relatively high pollution levels. Like *M. persimilis*, it was able to colonise several of the exposed moss cushions (fig. 8A). This agrees well with its ability to survive high concentrations of SO₂ (chapter 3.1.1) and with its natural distribution along the urban-rural gradient (STEINER, 1994b). The absence of *P. acuminatus* s.l. in naturally growing moss cushions at the most polluted site "R" (STEINER, 1994b) indicates, however, that this species is less pollution tolerant than *M. persimilis*.

Tylocephalus auriculatus, *Prionchulus muscorum*, *Echiniscus blumi*, *M. hufelandi*, *M. cf. artipharyngis* and *Hypsibius oberhaeuseri* persisted at the most polluted site "R" (annual mean values of SO₂: 47 µg/m³; NO₂: 87 µg/m³) for 28 months (fig. 8). In fumigation experiments (chapter 3.1.1), *E. blumi*, *M. hufelandi* and *M. cf. artipharyngis* were able to persist for 18 months at high treatment levels (585, 585 and 195 µg/m³, respectively). However, of the species mentioned above, only *H. oberhaeuseri* was found in naturally growing moss cushions at the high

traffic site "R", whereas *M. hufelandi*, along with *T. auriculatus* and *P. muscorum*, were mainly restricted to rural sites with low pollution levels (STEINER, 1994b). These contrasting results could be due 1) to the relatively short duration of both the fumigation and exposure experiments, i.e. a steady state corresponding to conditions prevailing in naturally growing moss cushions under the same air quality conditions was not yet reached; 2) by exposing the fauna together with the required microflora (within tegulous moss cushions), several species can survive at sites where they were missing in natural communities; 3) the combination of pollutants, as well as interactions with other stress factors can lead to opposing species responses, even if the annual mean values of the pollutants are very similar.

MICROCLIMATIC CONDITIONS AND OTHER FACTORS

The ranking of the exposure sites based on gas concentrations did not correlate with the ranking from low to high impact of the faunal response (fig. 8). Thus, the observed effects may have been due to differences in microclimatic conditions and/or in the substrata supporting the tiles (figs. 9 and 10).

Effects of the substrata supporting the tiles and of microclimatic conditions are closely related. The mechanisms by which the substratum influences the fauna are presumably via metal toxicity, temperature of the tiles and the moisture content of the moss cushions. Solar radiation can heat up roof tiles to over 40°C (VON DER DUNK, 1988b). Tiles exposed on unshaded metal sheets (sites "F", "D", "K" and "Tä") were presumably subjected to equivalent or even higher maximum temperatures in the summer months. These metal sheets were deprived of algae, lichens, mosses and consequently of the fauna associated with lower plants. The absence of a nearby species pool inhibits the colonisation of moss cushions exposed on these substrata. Therefore, immigration from the surroundings was a priori expected to be lower at sites where the tiles were exposed on metal sheets than at the other exposure sites. On concrete ("C", "Rä", "R" and "Ks") and boards ("T"), the presence of lichens indicated more favourable microclimatic conditions. Flat roofs covered with gravel ("Y" and "Z") were covered with an abundant moss flora. Together with the all day shaded site "L" (asbestos sheets with a well developed lichen flora), these sites probably provided the most favourable conditions for moss-invertebrate associations.

In fig. 9, the exposure sites are arranged along a moisture gradient, based on assumed daily solar radiation and on characteristics of the substratum supporting the tiles. Drastic effects of habitat disturbance are obvious at the control site "F". Tiles at site "F" were exposed on zinc sheets in front of a southern-faced wall. Drought, heat and/or zinc toxicity could thus be responsible for the rapid population decline in the summer of 1982. Effects of air pollution can be excluded, since the exposure location was only ten meters away from the roof on which all the tiles had been collected. Zinc sheets appeared to have detrimental effects on nematodes and tardigrades also at site "D". Almost all species were completely reduced until the first sampling in September 1982, although pollution ratings at the rural site "D" were considerably lower than at site "F" (fig. 8). This confirms the major role of zinc toxicity and/or heat in reducing

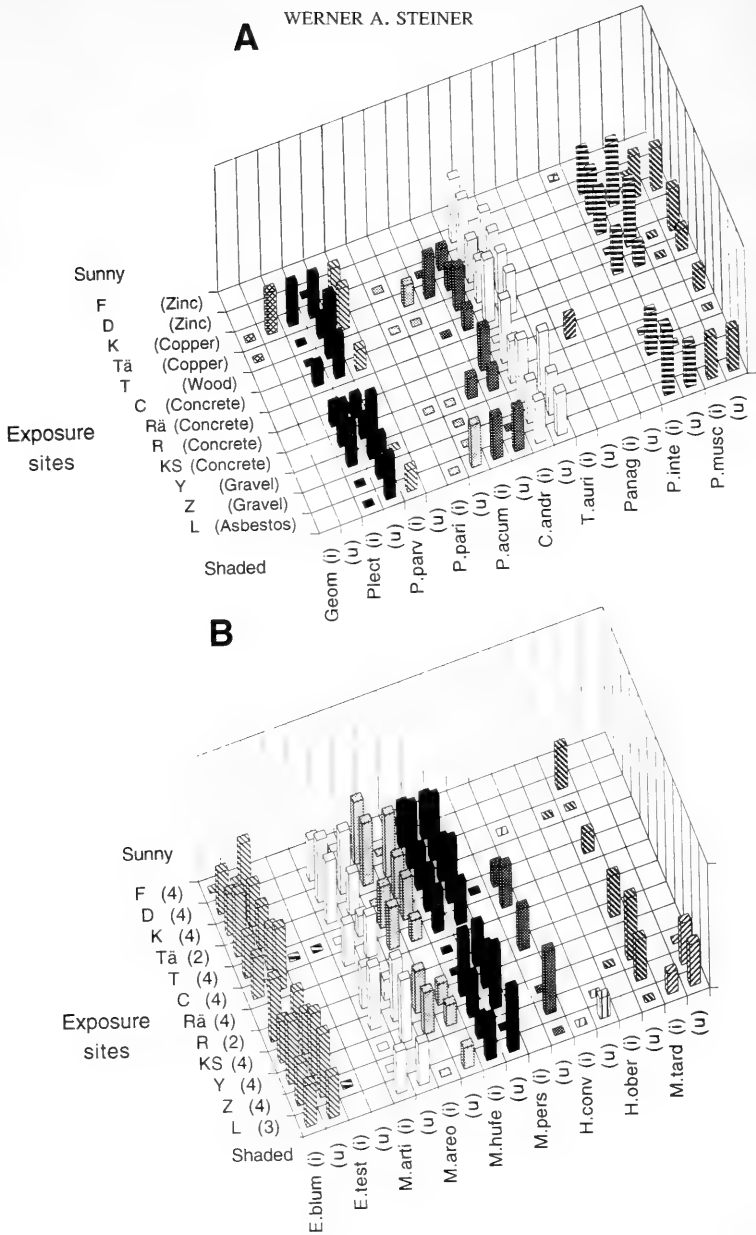


FIG. 9

Site specific changes in the abundance of (A) nematode and (B) tardigrade taxa (individuals/cm²; median) in moss cushions of the main exposure series. Sites are arranged according to microclimatic conditions and to substratum (indicated in A). Abbreviations for exposure sites and taxa are explained by STEINER (1994a); and in fig. 8, respectively. Numbers posterior to site abbreviations in (B) denote the number of tiles used to define the ultimate species composition. (i) = initial composition; (u) = ultimate composition; sunny: moss covered tiles exposed all day to sunlight; shaded: tiles shaded all day. Abundance values are explained in fig. 8.

the aquatic fauna. Moss cushions exposed on copper sheets ("K" and "Tä") were characterised by a very similar ultimate species composition (fig. 9). This suggests that the fauna was more strongly influenced by the substratum than by air quality, which differed considerably between the two exposure sites (fig. 8). Toxicity of Cu^{++} on nematodes is well documented (ALPHEY & BROWN, 1987). The rapid and almost complete extinction of nematodes and tardigrades at site "Rä" (May to September 1982) was presumably also influenced by copper. At this site, the tiles were exposed partly under a roof covered with copper sheets. Since pollution ratings at site "Rä" were lower than at site "R" – where several species persisted for 28 months – copper dissolved in downpours is likely to have caused the strong faunal reduction.

The relative importance of different environmental factors becomes evident at sites where the tiles were exposed on concrete. Exposure sites "C" and "T", although receiving more solar radiation than "Rä", "R" and "KS", were characterised by a higher ultimate diversity (fig. 9). This is taken as evidence that exceedingly high pollution ratings (site "R"), along with metal toxicity ("Rä", "F" and "D"), have a stronger impact on the moss-dwelling fauna than drought.

Favourable microclimatic conditions and the presence of lower plants are most probably responsible for the high ultimate diversity at the sites "Y", "Z" and especially at "L" (fig. 9). The exceedingly high number of surviving species at site "L" and the relatively high proportions of the predatory species (i.e. *P. intermedia*, *P. muscorum* and *Milnesium tardigradum*) are most likely a consequence of a favourable microclimate (shade) and the presence of a large species pool (immigration or re-immigration of species) in the resident lichen flora.

ROTIFERS AND ARTHROPODS

Rotifer numbers were almost unaffected by the factors that almost completely reduced the nematode and tardigrade fauna at the sites "F" and "Rä". At all the exposure sites, the abundance of rotifers remained the same size throughout the exposure period. This is in contrast to findings of the fumigation experiments, in which the rotifers had a similar response pattern to the nematodes (chapter 3.1.2).

The most abundant arthropod species at the end of the exposure period were *Scutovertex* cf. *sculptus*, *Trhypochthonius tectorum*, *Trichoribates* cf. *trimaculatus* and *Xenylla brevisimilis*. These species (all except *T. tectorum*) persisted at the polluted sites "R" and "T", and are resistant to SO_2 pollution (chapter 3.1) and drought (SMRŽ, 1992). The high pollution tolerance of *T. cf. trimaculatus* is confirmed by findings of a faunistic survey, showing that this mite occurs frequently in natural moss cushions at polluted sites (STEINER, 1995). No surviving arthropods were detected in moss cushions exposed on metal sheets of the urban site "Rä" and the rural sites "Tä" and "D". Since rural moss cushions were usually richer in oribatid species than urban mosses (STEINER, 1995), microclimatic conditions and/or damage by zinc and copper sheets must account for the observed extinction. As noted for the aquatic fauna, immigration of species was conspicuous at site "L", where species richness

increased during the exposure period. Arthropod numbers at the other sites were too small to investigate faunal response to environmental factors.

SUPPLEMENTARY EXPOSURE EXPERIMENTS

Comparison of supplementary and main exposure experiments reveals a similar response pattern. In agreement with the main exposure experiments, many taxa survived even at the most polluted site "R" (fig. 10), and the sites "F" and "Rä" were characterised by a relatively poor fauna. From the presence of similar faunal responses at the high traffic site "Rä" and the control site, it is evident that factors other than air quality are important in shaping the communities. For example, microclimatic effects (shade all day) and/or the presence of a species pool were most probably responsible for the richest ultimate fauna (83% of all the species initially counted) at site "L".

As compared with the main exposure experiments, the faunal reduction at the sites "F" and "Rä" was less expressed in the supplementary exposure series. This can be explained by the shorter exposure period and by the fact that these experiments started in September, when the temperature was relatively low and humidity relatively high. The main exposure series, in contrast, started in May, and the fauna experienced relatively high temperatures in the first period of exposure. Another difference to the main exposure experiments concerns *M. persimilis*. This pollution tolerant species only invaded moss cushions at the moderately polluted site "L". Since in the main exposure experiments *M. persimilis* was usually first recorded after an exposure period of 16 months, it is assumed that the exposure period of 12 months was too short for *M. persimilis* to get established. *Aphelenchoides* spp., typical of polluted moss cushions in the faunistic survey (STEINER, 1994b), was present at both polluted and unpolluted exposure sites (fig. 10).

The dominant species surviving at the most polluted site "R" were *P. acuminatus* s.l. and *H. oberhaeuseri* (fig. 10), two species shown to be relatively resistant to air pollution (STEINER, 1994b). *Chiloplectus* cf. *andrassyi*, a promising indicator species of air quality (chapter 3.1; Steiner, 1994b), was mainly confined to the less polluted sites. At site "Tä", *C.* cf. *andrassyi*, along with *Geomonhystera* sp. and *M.* cf. *artipharyngis*, most probably invaded from the simultaneously exposed tegulous moss communities of the main exposure series. *Milnesium tardigradum* – typical of the most humid sites in the main experiment (fig. 9) – was again confined to the shaded moss cushions at site "L".

Further analysis of the factors influencing the aquatic fauna seems arbitrary as the number of exposure sites was low.

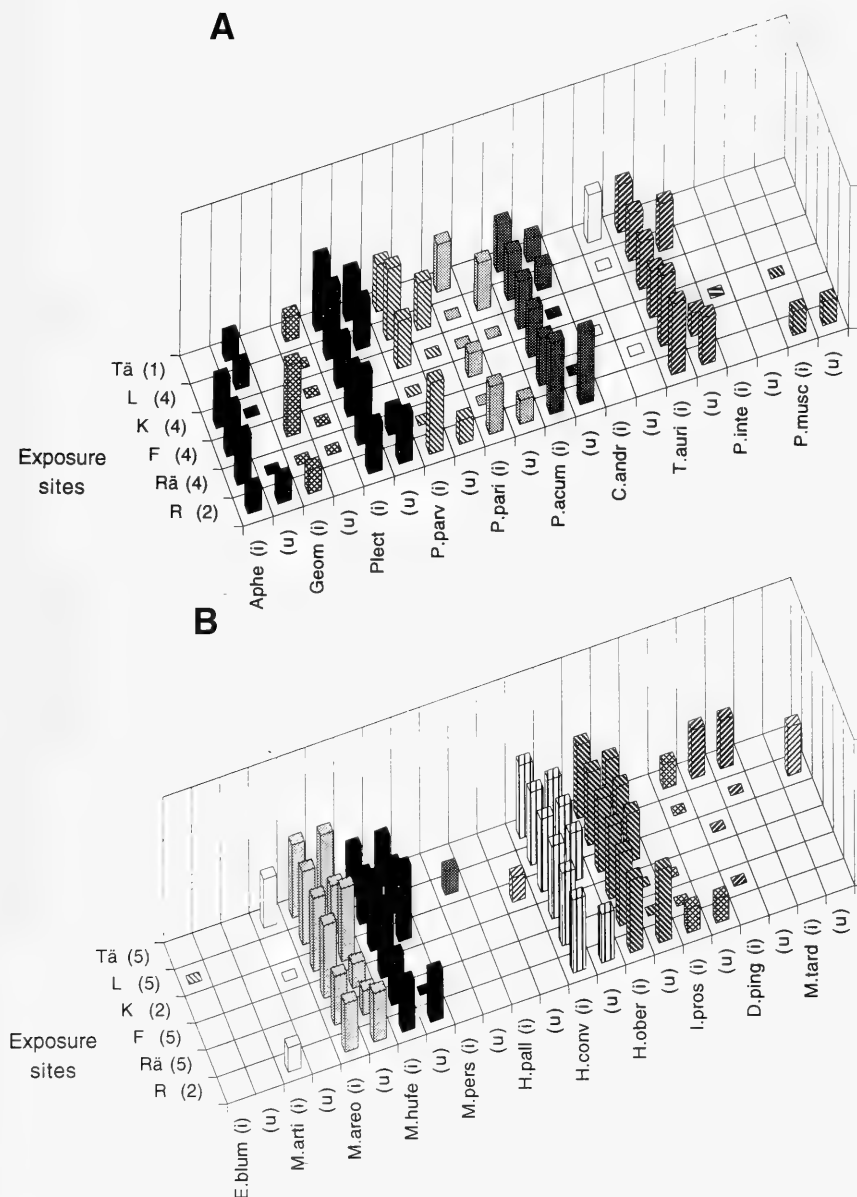


FIG. 10

Site specific changes in the abundance of (A) nematode and (B) tardigrade taxa (individuals/cm²; median) in moss cushions of the supplementary exposure series. Exposure lasted 16 months. Sites are arranged according to NO₂ levels. Abbreviations for exposure sites and NO₂ levels are explained by STEINER (1994a); and in fig. 8, respectively. Numbers following site abbreviations denote in (A) the number of tiles used to define the ultimate species composition; in (B) the sample size [cm²] used to define the ultimate species composition. (i) = initial composition; (u) = ultimate composition; Aphe: *Aphelenchoides* sp.; D.ping: *Diphascon pingue*; H.pall: *Hypsibius pallidus*; I.pros: *Isohypsibius prostomus*. Abbreviations for other taxa and abundance values are explained in fig. 8.

4 CONCLUSIONS

Results of the fumigation experiments demonstrate that the effects of SO_2 are dose-dependent and taxon specific. The abundance of nematodes, tardigrades and rotifers, as well as species richness of the two former taxa, was invariably lowest at the highest SO_2 concentration ($585 \mu\text{g}/\text{m}^3$). In the other treatments, however, species richness of nematodes and tardigrades varied independently of SO_2 concentrations and is thus an unsuitable community parameter for the analysis of SO_2 effects. The abundance of nematodes and rotifers decreased consistently with increasing SO_2 levels, and could therefore be used to indicate impacts of SO_2 pollution. Tardigrades reached largest numbers at intermediate SO_2 concentrations (65 and $195 \mu\text{g}/\text{m}^3$). A general no-effect level cannot be assessed, since even the smallest SO_2 concentration ($65 \mu\text{g}/\text{m}^3$) was associated with a decrease in nematode numbers. Long-term fumigation with SO_2 significantly decreased the pH of the moss cushions. These changes in pH, along with SO_2 (and/or formation products), influenced the aquatic fauna either directly or indirectly through changes in the microflora.

The results from exposure experiments usually coincided with findings of the fumigation experiment and the faunistic survey (STEINER, 1994b). The influence of site specific air quality was modified by effects of different microenvironmental conditions and/or by the type of the substratum supporting the tiles. The analysis of comparative importance of the environmental factors suggested that faunal changes were determined less by heat (and/or the rapid changes of humidity and temperature) than by metal toxicity. However, because of the complex nature of the environmental factors at the exposure sites (e.g. mixture of air pollutants, metal toxicity, microclimate), fumigation experiments with NO_2 would be necessary to draw final conclusions about the observed changes of the aquatic fauna. If the modifying effect of the microclimate and of the substratum can be excluded, the transplantation of standardised moss-invertebrate associations could be a convenient on-site method for assessing the consequences of air pollution for soil environments.

Combining the findings of fumigation experiments, exposure experiments and the faunistic survey (STEINER, 1994b), a set of three species arose to act as indicators of air pollution. The nematode *Chiloptectus* cf. *andrassyi* appears to be the most sensitive species. Populations of *C. cf. andrassyi* disappeared at the most polluted exposure sites. They decreased significantly with increasing SO_2 concentrations in the fumigation experiments as well as with increasing air pollution in the field (STEINER, 1994b). *Paratripyla intermedia*, another nematode species, was significantly reduced with increasing pollution in the field (STEINER, 1994b), and in the highest SO_2 treatment after a very short fumigation period (tab. 2). It was absent at the polluted sites "R" and "T" in natural communities (STEINER, 1994b), and also in the exposed communities at site "R" (last sampling). The tardigrade *Macrobiotus persimilis*, in contrast, is typical of sites with relatively high levels of NO_2 . At the urban roadside sites "R" and "T", *M. persimilis* was present in exposed as well as in naturally growing mosses (STEINER, 1994b). It invaded several tegulous mosses exposed at urban sites and got established there. This shows its power of dispersal and its ability to endure high pollution ratings.

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Über Vorkommen und Verbreitung von *Amaurobius*-Arten in Peloponnes und Ägäis (Araneida: Amaurobiidae)

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The genus *Amaurobius* in Peloponnese and Aegean Islands, Greece, (Araneida: Amaurobiidae). - Four new species of *Amaurobius* from Peloponnese, Attica and the Aegean Islands are described and illustrated (♂ ♀): *A. longipes* n. sp. from Mt. Parion, *A. timidus* n. sp. from Mt. Erimanthos, *A. atticus* n. sp. from Attica, *A. deelemanae* n. sp. from Naxos Is. *A. longipes* and *A. timidus* appear to be monotypic. *A. deelemanae* is polytypic, with close relatives on Rhodos and Crete, while *A. atticus* probably forms a superspecies together with *A. pelops* Thaler & Knoflach from NE-Peloponnese, Feneos basin. The four *Amaurobius* species now known from Peloponnese also occur without sympatry in isolated mountain groups. Possibly separation of distribution areas and isolation due to various climatic and geological changes have favoured speciation. A key proposed in 1993 is modified to include the new species. Sexually dimorphic hairs on the forelegs of the males are also illustrated.

Key-words: Araneida - Amaurobiidae - Greece - Taxonomy - Distribution - Sexual dimorphism.

EINLEITUNG

Aus der im glazial devastierten Mitteleuropa nördlich der Alpen im wesentlichen durch vier expansive Arten vertretenen Gattung *Amaurobius* waren aus Griechenland nur drei Arten bekannt (BRISTOWE 1934, HADJISSARANTOS 1940). Dagegen kommen im Gebiet der glazialen Refugien am Südrand der Alpen und im nördlichen SE-Europa ca. 12 endemische, teilweise als Rückwanderer einzustufende Arten vor. Doch ist die Artenarmut Griechenlands nur scheinbar. Wie die rezenten Aufsammlungen zeigen, sind auch in den Wäldern der Gebirge des Peloponnes und in der Ägäis kleinräumig verbreitete *Amaurobius*-Formen vorhanden, erste Ergebnisse in THALER & KNOFLACH

(1991, 1993). Anders als bei der sehr konservativen Gattung der Ctenizidae *Cyrtocarenum* (DECAE 1986, 1993) scheinen Arealzerreißung und Isolation im Gefolge der wechselhaften geologischen und klimatischen Ereignisse bei Amaurobiidae auch in Griechenland zu Speziation geführt zu haben. Im Anschluß an die Beschreibung von vier neuen Arten geben wir einen vorläufigen Überblick.

DANK: Dr. Christa L. Deeleman-Reinhold (Ossendrecht) überliess uns ihre *Amaurobius*-Fänge in Attika und Ägäis zum Studium, weitere Belege haben uns Dr. Fulvia Bertrandi (Trieste) und A. Ausobsky (Bischofshofen) zur Verfügung gestellt. Prof. Dr. S. Bortenschlager eröffnete uns den Zugang zu einem REM (Leitz-AMR 1000), S. Tatzreiter hat die REM-Aufnahmen angefertigt und ausgearbeitet. UD Dr. W. Resch gab uns Hinweise zur Geologie der Region, Dr. P. Merrett überprüfte das Abstract. Ihnen allen sei sehr herzlich gedankt.

DEPONIERUNG: CTh Arbeitssammlung Thaler; MHNG Muséum d'Histoire naturelle, Genève; NMB Naturhistorisches Museum Basel; NMW Naturhistorisches Museum Wien. Funde ohne Angabe eines Sammlers von Verf.

ABKÜRZUNGEN: E Embolus, K Konduktor, MA, PA, RA mittlere, prolaterale bzw. retrolaterale Apophyse der ♂ Taster-Tibia, MP Mittelplatte (Epigyne), TA Tegularapophyse, TF Tegularfortsatz.

BESCHREIBUNGEN

Amaurobius longipes n. sp.

(Figs 1, 3-4, 18, 28, 41-43, 54)

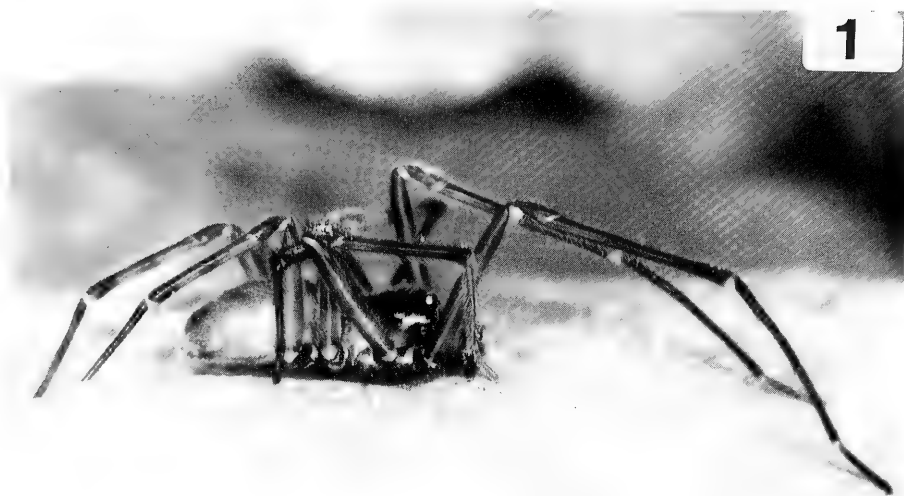
Fundorte und Material: Peloponnes: Paron, Paßhöhe westl. Kosmas ca. 1000 m, Tannenwald, Netze in Spalten in Erdböschungen und unter überwachsenen Steinen; 2♀ 28. Sept. 1985, 5♀ 26. Sept. 1992 (zusätzlich Totfunde [1♂ 2♀] und Juv. [10♂ 5♀ Reifehäutungen Jan. bis Juli 1993]). Polidroso 1200 m, ebenso 5♀ 28. Sept. 1992. Holotypus ♂ MHNG, Paratypen MHNG (2♂ 4♀), NMB (2♂ 2♀), NMW (2♂ 2♀), CTh (3♂ 4♀).

Diagnose: Von den übrigen Arten in Peloponnes und Ägäis durch die Verlängerung der ♂ Vorderbeine auffällig verschieden. Tibialapophysen Fig 18, TF stumpf-kegelig, Embolus kurz, Fig 3. Epigyne Figs 41-42. Abweichend wohl auch der Lebenszyklus.

Etymologie: lat., als Hinweis auf die Beine des ♂.

♂ ♀: Dimensionen [♂ (♀), n = 10 (18), mm]: Gesamtlänge 8-10 (7.5-12.5). Prosoma-Länge 4.1-4.6 (3.3-5.4), Prosoma-Breite 2.9-3.2 (2.2-3.7), Länge Femur I 6.1-6.6 (2.7-4.6), beim ♂ 1.5, beim ♀ 0.8-0.9 der Prosoma-Länge. Prosoma und Beine gelb-bräunlich, Caput und Cheliceren braun-schwärzlich, Opisthosoma grau, ungezeichnet. Beine ungeringelt. Vorderbeine des ♂ auffällig verlängert, ihre Tibien, Metatarsen und Tarsen wie bei den anderen Arten allseitig mit schräg abstehenden Haaren (Figs 1, 54).

♂-Palpus: Apophysen der Taster-Tibia Figs 18, 28, MA ohne Nebenzahn. Cymbium und Bulbus Figs 3-4, TF stumpf-kegelig, wenig vorragend, TA mit basaler Schuppe, Embolus verhältnismäßig kurz, gleichmäßig gebogen.



FIGS 1-2

Amaurobius longipes n. sp. (1, Parnon, Reifehäutung 12. Feber 1993), *A. erberi* (Keyserling) (2, I Trieste: Aurisina, 12. Jan. 1994, leg. Brandi). Habitus ♂.

Epigyne-Vulva: Figs 41-43. Einführungsgänge kurz, Rezeptakel sitzend, weit voneinander getrennt. Seitenplatten zahnförmig.

Beziehungen: *A. longipes* n. sp. zeichnet sich vor den übrigen Arten der Gattung durch ungewöhnliche Verlängerung der ♂-Vorderbeine aus; zudem scheint der Lebenszyklus keineswegs "diplochron" zu verlaufen. Verf. vermögen keine näheren Beziehungen anzugeben. Sie suchen diese auch nicht bei den bereits in Vorderasien vorhandenen Phyxelidinae (GRISWOLD 1990): Innenseite der Palpenfemora ohne Stridulationsborsten, Cymbium retrolateral/proximal eingewölbt, Tibien und Metatarsi I ohne die Sonderbildungen der Phyxelidinae, bei Ähnlichkeit zu manchen Vidoleini, tarsale Becherhaare vorhanden. Die merkwürdige Behaarung der ♂ Vorderbeine ist auch bei den anderen *Amaurobius*-♂ vorhanden.

Verbreitung, Zyklus: SE-Peloponnes, Tannenwälder des Parnon-Gebirges 1000-1200 m. Lebenszyklus abweichend von den übrigen Arten: im Sept. wurden nur ♀ mit Befruchtungszeichen, jedoch noch ohne Eikokon angetroffen. BK fand 2 tote ♀ inmitten ihrer aggregierten Nachkommen - offensichtlich von diesen konsumiert (HOLM 1940, TAHIRI *et al.* 1989). In Gefangenschaft fertigte 1 ♀ einen Kokon am 25. Feber; bereits solitäre Jungtiere erreichten nach 2-3 Häutungen bei haltungsbedingter Streuung die Geschlechtsreife: 10 ♂ am 20. Jan., 12. Feb., 10. März (2♂), 28. März, 5. April (3♂), 20. April, 7. Juni; 5 ♀ am 26. April (3♀), 1. Juni, 30. Juli. Demnach scheint sich folgender Zyklus zu ergeben: Reifehäutung und Kopula in Frühling-Frühsommer (genauer Zeitpunkt ist noch festzulegen), ♂ kurzlebig, ♀ gelangen erst im folgenden Frühjahr zur Eiablage, zwei Überwinterungen durch Inadulte.

***Amaurobius timidus* n. sp.**

(Figs 5, 6, 19, 29, 39-40)

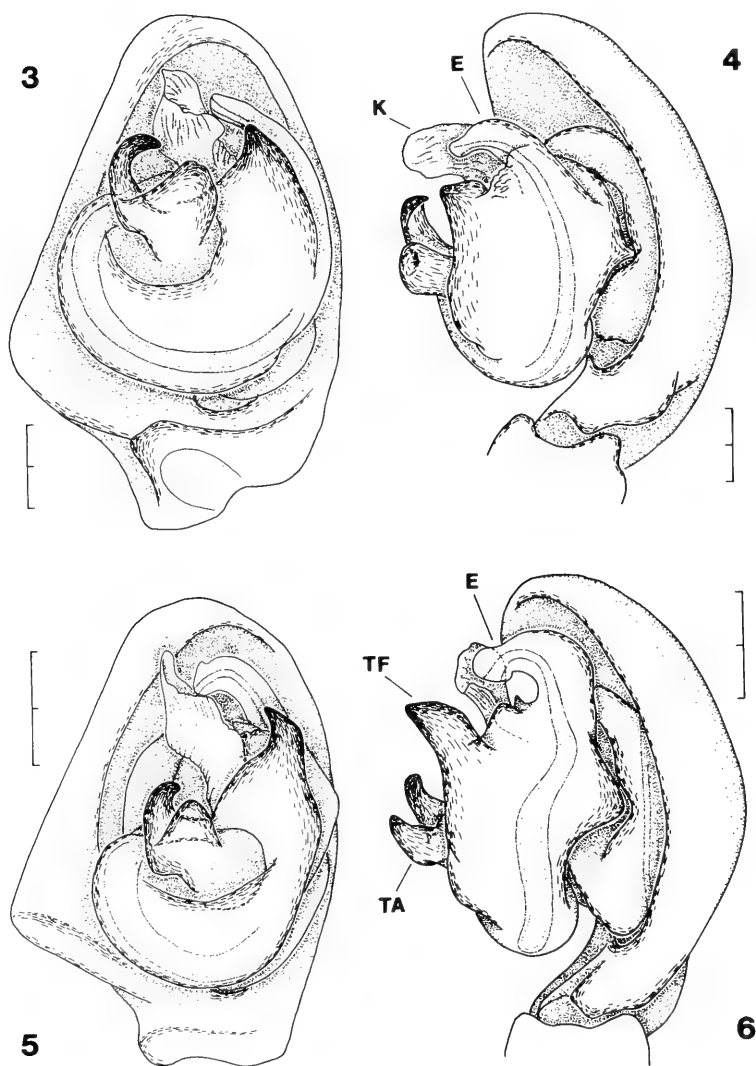
Fundorte und Material: Peloponnes: Erimanthos, Kalendzi 1200 m, steiler Hang in lichtem Tannenwald, Nadelstreu ohne Unterwuchs, unter Steinen (Kalk) und Fallholz; 1 ♀ NMW 27. Sept. 1991, 3♂ 4♀ 1 sad. ♂ MHNG (1♂ Holotypus 1♂ 2♀), CTh (1♂ 2♀) 20. Sept. 1992. Es ist nur der Holotypus bezeichnet, die übrigen Exemplare gelten als Parotypen.

Diagnose: Unter den Arten mit spitz abstehendem TF gekennzeichnet durch die Ausbildung der Tibialapophysen (Fig. 19) und Bulbusmerkmale: Embolus, TA. Epigyne: Figs 39-40.

Etymologie: lat. *timidus*, *a, um*, furchtsam.

♂ ♀: Dimensionen [♂ (♀), n = 3 (4), mm]: Gesamtlänge 5.2-6.2 (6.0-6.8), Prosoma-Länge 2.6-2.8 (2.9-3.5), Prosoma-Breite 1.8-1.9 (1.9-2.3), Länge Femur I 2.4-2.6 (2.0-2.4), beim ♂ 0.90, beim ♀ 0.68 der Prosoma-Länge. Prosoma und Beine gelbbraunlich, Opisthosoma ventral und lateral schwärzlich gefleckt, dorsal mit Herzfleck und Winkelflecken. Beine ungeringelt.

♂-Palpus: Charakteristisch die Apophysen der Tibia, Figs 19, 29: PA triangular, mit breiter Basis, schrägem Außenrand und eingewölbter Ventralseite, MA kurz, zahnförmig ohne Nebenzahn, RA daumenförmig abstehend. Cymbium und Bulbus: Figs 5-6. TF spitz-triangular, TA gedrunken, mit kurzem Endast und breitem Basalfortsatz, Embolus sichelförmig.



FIGS 3-6

Amaurobius longipes n. sp. (3-4, Parnon), *A. timidus* n. sp. (5-6, Erimanthos: Kalendzi). ♂-Taster von ventral (3, 5) und von prolateral (4, 6). — Maßstäbe: 0.20 mm.

Epigyne-Vulva: Figs 39-40. Mittelplatte schmal-spangenförmig (auch in Aboral-Ansicht), Vorderecken der Epigyne nicht nach vorn ausgerandet, Receptacula weit getrennt, sitzend.

Beziehungen: Von den benachbarten Arten scheint *A. pelops* stärker abzuweichen: MA mit Nebenzahn, TA lang-angezogen, Position der Receptacula weiter vorn. In diesen drei Merkmalen stimmt *A. timidus* n. sp. mit *A. paon* überein - der allerdings durch die starke Entwicklung der PA markant gekennzeichnet ist.

Verbreitung: NW-Peloponnes, nur vom Locus typicus bekannt: Tannenwald des Erimanthos-Gebirges ca. 1200 m. Aufgesammelt wurden frisch gehäutete Exemplare: Jahreszyklus anscheinend diplochron wie bei den Arten in Mitteleuropa.

Amaurobius paon Thaler et Knoflach, 1993

Fundort und Material: Peloponnes, Taigetos, Motel Taigetos nahe Lipovouni ca. 1400 m, in hochstämmigen Kiefernwald mit reicher Nadelförmigkeit, unter Fallholz und Rindenstücken, 3♂ 4♀ MHNG (2♂ 2♀), CTh (1♂ 2♀) 23. Sept. 1992. Ebenda, Tannenwald auf Kalk, Moosunterwuchs, unter Stein, 1♀ NMW 23. Sept. 1992.

Der neue Nachweis im nördlichen Taigetos ist in einer Entfernung von ca. 25 km vom Locus typicus erfolgt. Die Exemplare entsprechen der Erstbeschreibung.

Amaurobius cf. pelops Thaler et Knoflach, 1991

(Figs 7, 9, 25, 33, 37-38)

Fundorte und Material: N-Peloponnes, Strecke Feneos-Likouria, Feneos-Paß, Ostabhang ca. 900 m, unter Steinen in lichtem Tannenwald, 7♂ 1 sad. ♂ 5♀ MHNG (3♂ 2♀), CTh (4♂ 3♀).

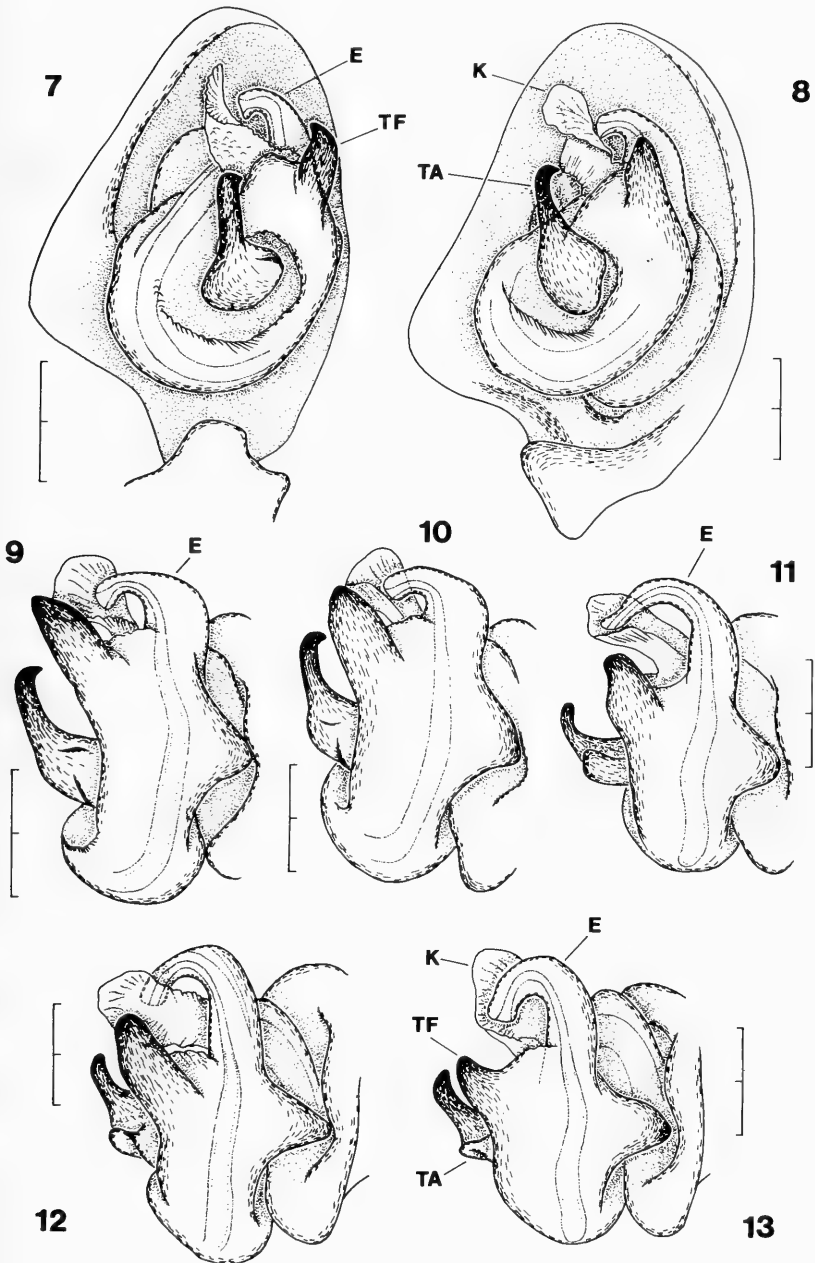
♂ ♀: Dimensionen [δ (φ), n = 6 (4), mm]: Gesamtlänge 5.3-6.2 (5.4-6.4), Prosoma-Länge 2.5-2.9 (2.7), Prosoma-Breite 1.8-2.0 (1.7-1.9), Länge Femur I 2.8-3.2 (1.9-2.0), beim ♂ 1.1, beim ♀ 0.73 der Prosoma-Länge. Färbung und Zeichnung wie bei *A. timidus* n. sp., Beine ungeringelt.

♂-Palpus: Apophysen der Tibia Figs 25, 33. PA länger als beim Holotypus, klingenförmig, dorsad in ein feines Spitzchen ausgezogen, Vorderrand der MA eingedellt, innen gleichmäßig gerundet und nicht fingerförmig verlängert. Cymbium und Bulbus wie beim Holotypus, TA mit schlankem Endast, ohne Basalfortsatz, Figs 7, 9.

Epigyne-Vulva: Figs 37-38, wie bei *A. pelops* s. str., Einführungsöffnungen vorn bogig begrenzt. Seitenplatte ohne Modifikation.

Diskussion, Beziehungen: Das Holotypus ♂ weicht trotz grundsätzlicher Übereinstimmung in der Ausbildung von PA und MA von den hier vorliegenden und diesbezüglich uniformen Exemplaren markant ab, Fig. 24 vs. 25. Diese wurden in nur ca. 10 km Entfernung vom Typusfundort gesammelt, die Fundorte sind durch die abflußlose Karstwanne des Feneos-Sees getrennt. Zur taxonomischen Bewertung sind weitere Untersuchungen nötig. Enge Beziehungen bestehen zu *A. atticus* n. sp. (Figs 7 vs. 8, 24-26).

Verbreitung: N-Peloponnes, bewaldete Berghänge der Umrandung des Beckens von Feneos.



FIGS 7-13

Amaurobius cf. *pelops* Thaler et Knoflach (7, 9, Feneos), *A. atticus* n. sp. (8, 10, Peania, Koutouki Cave), *A. deelemanae* n. sp. (11, Kreta: Perama; 12, Naxos: Apirathos, 13, Rhodos: Prof. Ilias). ♂-Taster von ventral (7-8), Bulbus von prolateral (9-13). - Maßstäbe: 0.20 mm.

Amaurobius atticus n. sp.

(Figs 8, 10, 26, 34)

Fundorte und Material: Attika, Peania, Koutouki Cave, 1♂ Holotypus MHNG, inad. 17. April 1984 [Reifehäutung am 17. Aug. 1984], C.L. Deeleman & P.R. Deeleman leg.

Diagnose: Größer als *A. pelops*; von der Vergleichsart durch die Konfiguration der Tibialapophysen (Fig. 34) verschieden.

Etymologie: lat. *atticus*, *a, um*; die Herkunft bezeichnend.

♂: Gesamtlänge 7.2, Prosoma-Länge 3.3, Prosoma-Breite 2.4, Länge Femur I 4.0 mm, Femur I 1.2 der Prosoma-Länge. Färbung und Zeichnung wie bei *A. timidus* n. sp., Beine ungeringelt.

♂-Palpus: Apophysen der Tibia Figs 26, 34. PA ähnlich wie bei cf. *pelops* klingenförmig und in ein feines Spitzchen ausgezogen, ihr Dorsalrand jedoch distad konvergierend; MA schmaler, vorn nicht eingebuchtet. Cymbium und Bulbus Figs 8, 10, TA modifiziert wie bei *pelops*, TF massiver wirkend als bei der Vergleichsart.

Beziehungen: Eng verwandt und wohl vikariierend mit der geographisch nächsten Art des N-Peloponnes *A. pelops*.

Verbreitung: Griechenland, Attika. Wohl nicht troglobiont, sondern eine hygrophile, auch in subterrane Lebensräume eindringende Freilandart.

Anmerkung: Die Zugehörigkeit von 2♀ vom selben Fundort (C.L. & P.R. Deeleman leg. 17. April 1984) scheint uns nicht eindeutig: Gesamtlänge 9.9, Prosoma-Länge (Breite) 3.8 (2.6), 4.6 (3.2), Länge Femur I 3.2, 3.4 mm, nur 0.8 der Prosoma-Länge. Färbung und Zeichnung ebenfalls wie bei *A. timidus* n. sp. Epigyne-Vulva: Figs 35-36. Einführungsöffnungen vorn bogig begrenzt, die Mittelplatte aber aborad wie bei *A. deelemanae* n. sp. stärker konvergierend, trapezförmig. - HADJISSARANTOS (1940) hat aus Attika "*A. erberi*" in Anzahl gemeldet: erst weitere Aufsammlungen werden über Identität und Verbreitung dieser Formen Aufschluß geben.

Amaurobius deelemanae n. sp.

Figs 12, 14, 22, 31, 46-47

Fundort und Material: Kykladen, Naxos, Apirathos, Fanariotissa spileon, 1♂ Holotypus MHNG, 1♂ 1♀ Paratypen MHNG, C.L. Deeleman & P.R. Deeleman leg. 23. April 1984. - Weitere Funde auf Kreta und Rhodos mögen distinkte Unterarten verkörpern:

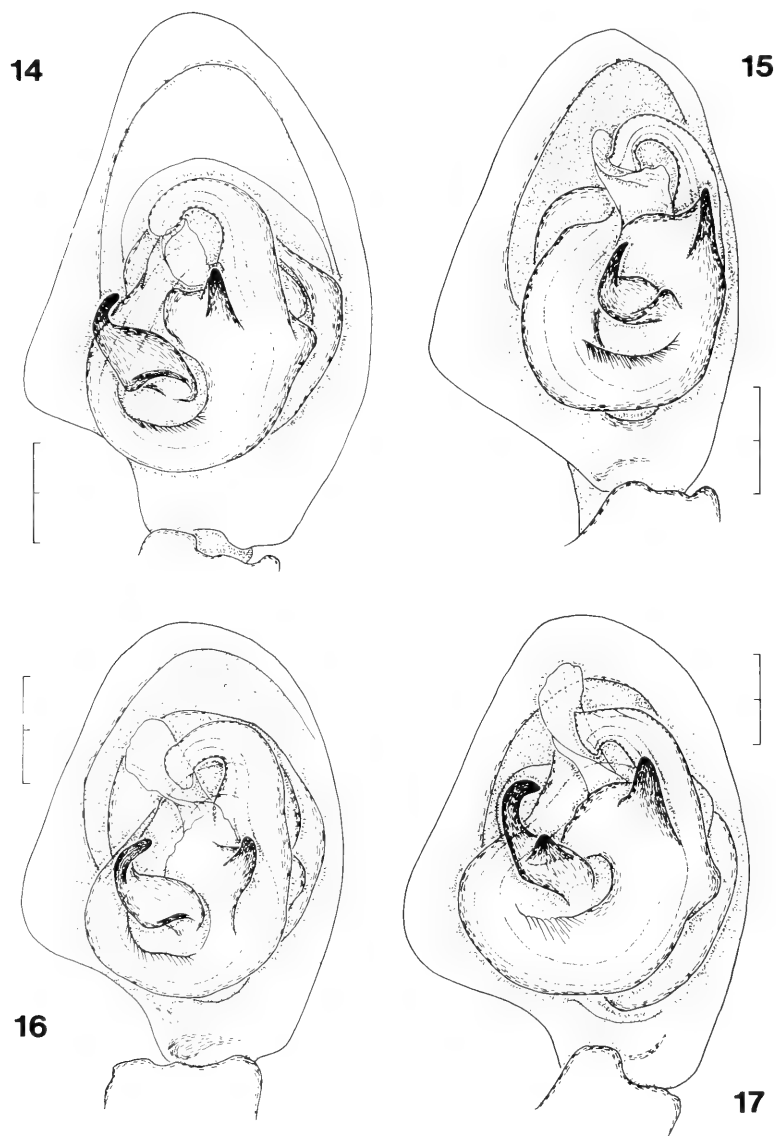
Kreta, Perama, unter Fallaub von *Platanus* an Bachlauf, 1♂ MHNG, C.L. & P.R. Deeleman leg. 22. März 1981. Ebenda, Perama (Rethymnon), 2♀ MHNG, P.R. Deeleman leg. 11. Feber 1981.

Dodekannes, Rhodos, Profiti Ilias 800 m, Kiefern, 1♂ 2♀ MHNG, C.L. & P.R. Deeleman leg. 10. April 1987.

Diagnose: Unter den Arten mit spitz abstehendem TF charakterisiert durch Verlängerung des Embolus und die spezielle Ausbildung der Tibialapophysen. Epigyne: Figs 46-47.

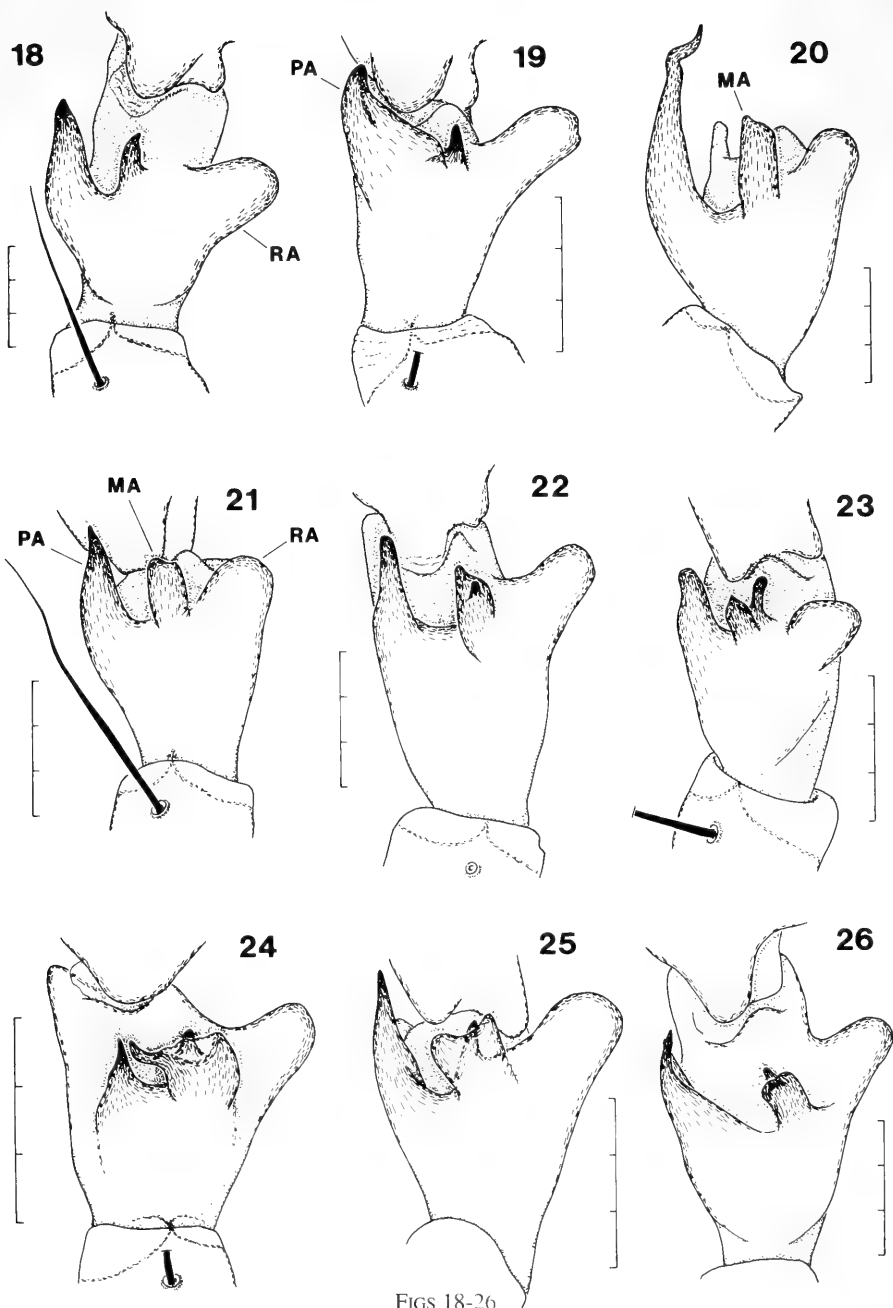
Etymologie: Frau Dr. C.L. Deeleman (Ossendrecht) zu Ehren benannt.

♂ ♀: Dimensionen [♂ (♀), mm]: Gesamtlänge 6.2, 6.8 (9.6), Prosoma-Länge 3.7 (4.2), Prosoma-Breite 2.7 (? , verformt), Länge Femur I 3.6 (3.0), beim ♂ 0.98, beim ♀ 0.72 der Prosoma-Länge. Prosoma und Beine bräunlich, Tibien mit Spuren einer Ringelung, Abdomen mit grauen Flecken.



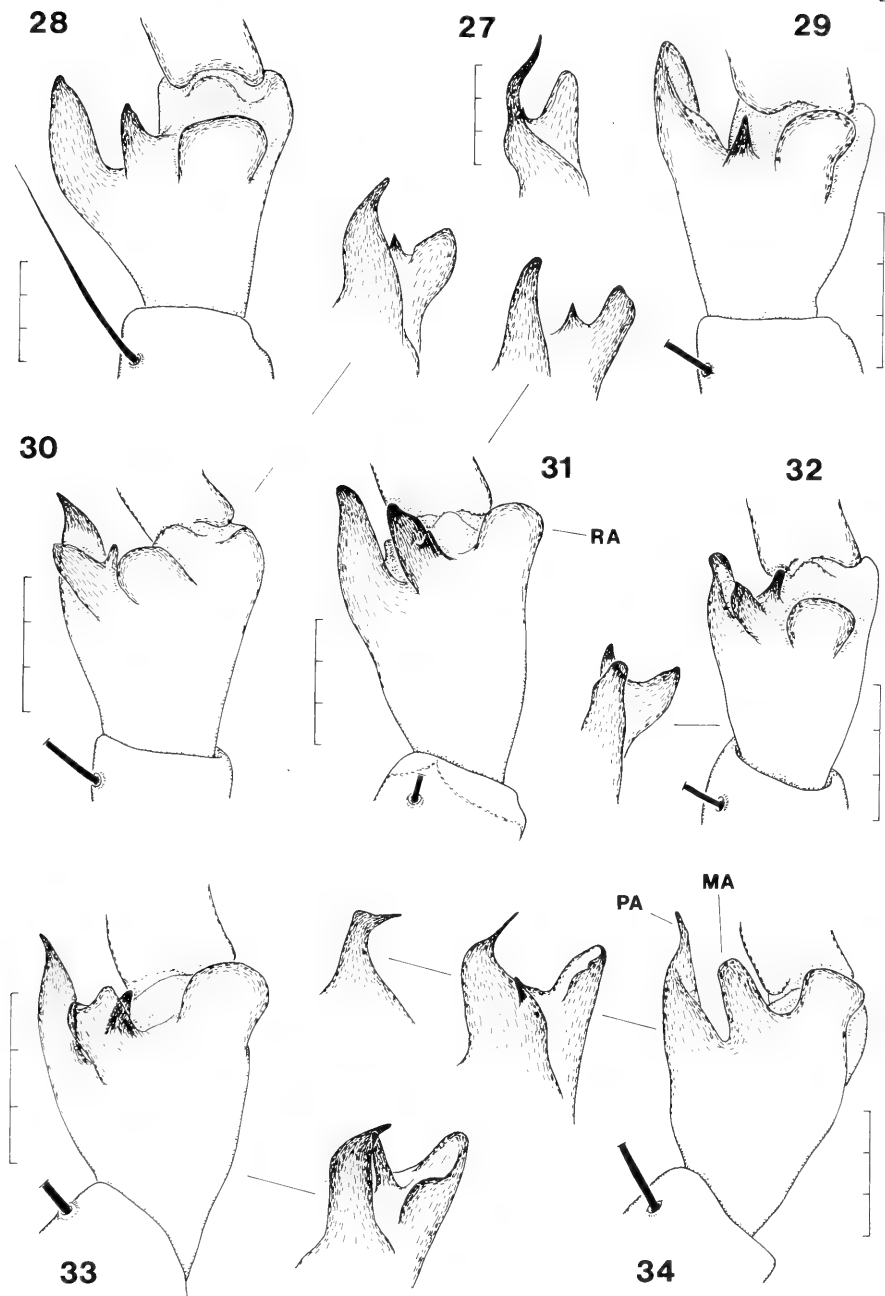
FIGS 14-17

Amaurobius deelemanae n. sp. (14 Naxos, 15 Kreta, 16 Rhodos [Fundorte wie bei Figs 11-13]),
A. erberi (Keyserling) (17, HR Istrien: Rovinij, 18. Okt. 1970). ♂-Taster von ventral (14-17). -
 Maßstäbe: 0.20 mm.



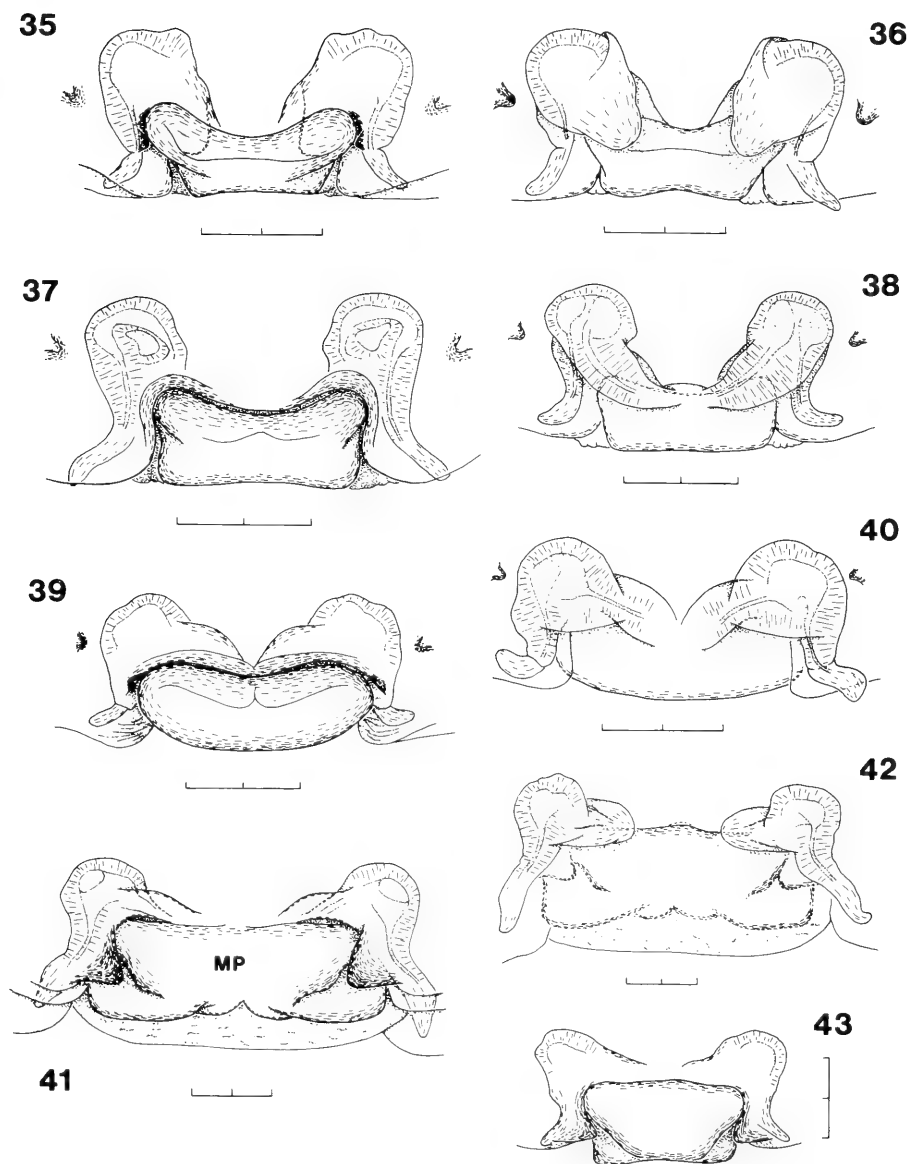
FIGS 18-26

Amaurobius longipes n. sp. (18), *A. timidus* n. sp. (19), *A. erberi* (Keyserling) (20), *A. deeleanae* n. sp. (21 Rhodos, 22 Naxos, 23 Kreta), *A. pelops* Thaler et Knoflach (THALER & KNOFLACH 1991, zum Vergleich), *A. cf. pelops* (25), *A. atticus* n. sp. (26); Fundorte siehe Figs 3-13. ♂-Taster von dorsal. - Maßstäbe: 0.30 mm.



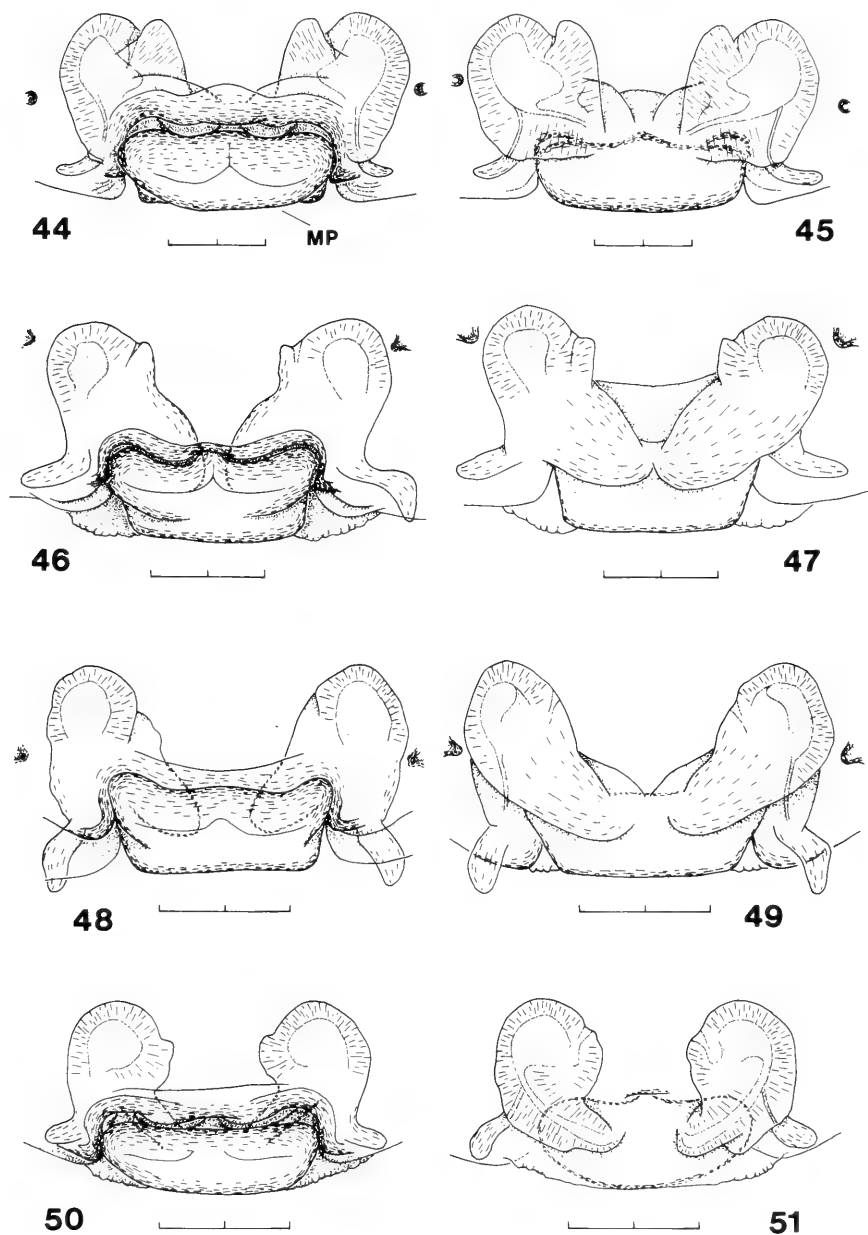
FIGS 27-34

Amaurobius erberi (Keyserling) (27), *A. longipes* n. sp. (28), *A. timidus* n. sp. (29), *A. deelemanae* n. sp. (30 Rhodos, 31 Naxos, 32 Kreta), *A. cf. pelops* (33), *A. atticus* n. sp. (34); Fundorte siehe Figs 3-13. ♂-Taster-Tibia von retrolateral (28-34), Apophysen der ♂-Taster-Tibia von prolateral (Nebenbilder und Fig. 27). - Maßstäbe: 0.30 mm.



FIGS 35-43

Amaurobius sp. (35-36, Peania, Koutouki Cave), *A. cf. pelops* (37-38), *A. timidus* n. sp. (39-40), *A. longipes* n. sp. (41-42 [Prosoma-Länge 5.4], 43 [Prosoma-Länge 3.7 mm]). Fundorte siehe Figs 3-8. Epigyne-Vulva von ventral und von dorsal (36, 38, 40, 42-43). - Maßstäbe: 0.20 mm.



FIGS 44-51

Amaurobius erberi (Keyserling) (44-45), *A. deelemanae* n. sp. (46-47 Naxos, 48-49 Rhodos, 50-51 Kreta). Fundorte siehe Figs 11-13, 17. Epigyne-Vulva von ventral und von dorsal (45, 47, 49, 51). - Maßstäbe: 0.20 mm.

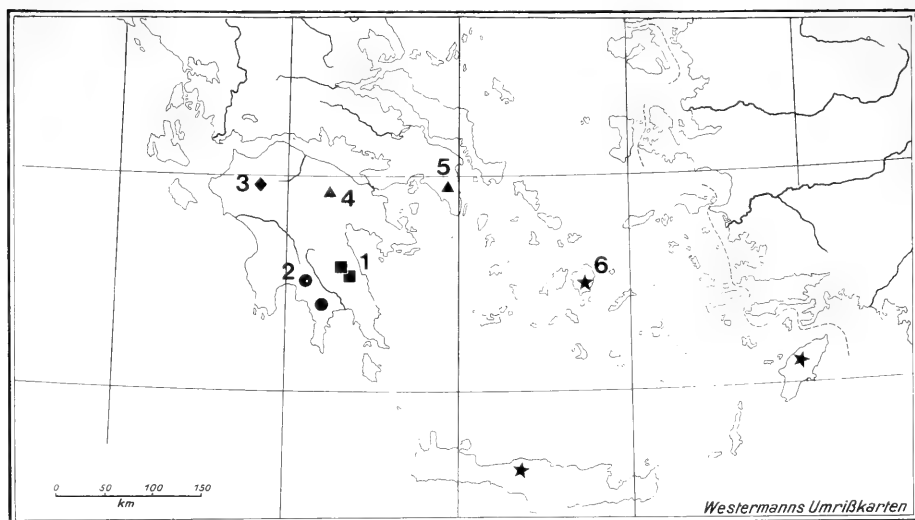


FIG. 52

Fundpunkte von Arten der Gattung *Amaurobius* (Amaurobiidae) in Peloponnes und Ägäis: 1 *A. longipes* n. sp., 2 *A. paon* Thaler et Knoflach, 3 *A. timidus* n. sp., 4 *A. pelops* Thaler et Knoflach und *A. cf. pelops*, 5 *A. atticus* n. sp., 6 *A. deelemanae* n. sp. (Locus typicus Naxos).

♂-Palpus: Apophysen der Tibia Figs 22, 31. MA ähnlich wie bei *A. erberi*, von dorsal schlank erscheinend, ca. 3 mal länger als breit, mit parallelen Seiten. PA klingenförmig. Cymbium und Bulbus Figs 12, 14. TF wie bei den Vergleichsarten, Tegularapophyse gedrunken, mit Basalfortsatz. Embolus länger als bei *A. erberi*, zunächst gerade nach vorn ragend, dann in nahezu rechtem Winkel nach retrolaterad gekehrt.

Epigyne-Vulva: Figs 46-47. Mittelplatte mit schmalen Ventralsaum, in Aboralansicht trapezförmig. Seitenplatten an der Umbiegungsstelle mit niederer Zahnbildung.

Beziehungen: In der Konfiguration der Tibialapophysen grundsätzlich mit *A. pelops* und *A. erberi* übereinstimmend; von beiden Arten durch die Form des Embolus verschieden, TA ähnlich wie bei *erberi*.

Verbreitung: Zwei in Details (MA, TF) abweichende ♂ von Rhodos und von Kreta deuten an, daß es sich bei *A. deelemanae* n. sp. um eine polytypische, auf den griechischen Inseln weiter verbreitete Art handelt. Zur Bewertung der Unterschiede sind weitere Befunde nötig. Entfernungen Naxos-Rhodos und Naxos-Kreta ca. 230, Kreta-Rhodos ca. 320 km. Möglicherweise kommt die Form auch auf dem Festland vor, siehe die zwei zusammen mit dem Holotypus von *A. atticus* n. sp. gesammelten ♀ (Figs 35-36) und die Diskussion bei dieser Art. Auch bei *A. deelemanae* n. sp. scheint es sich um eine hygrophile, gelegentlich in Höhlen eindringende Freiland-Art zu handeln.

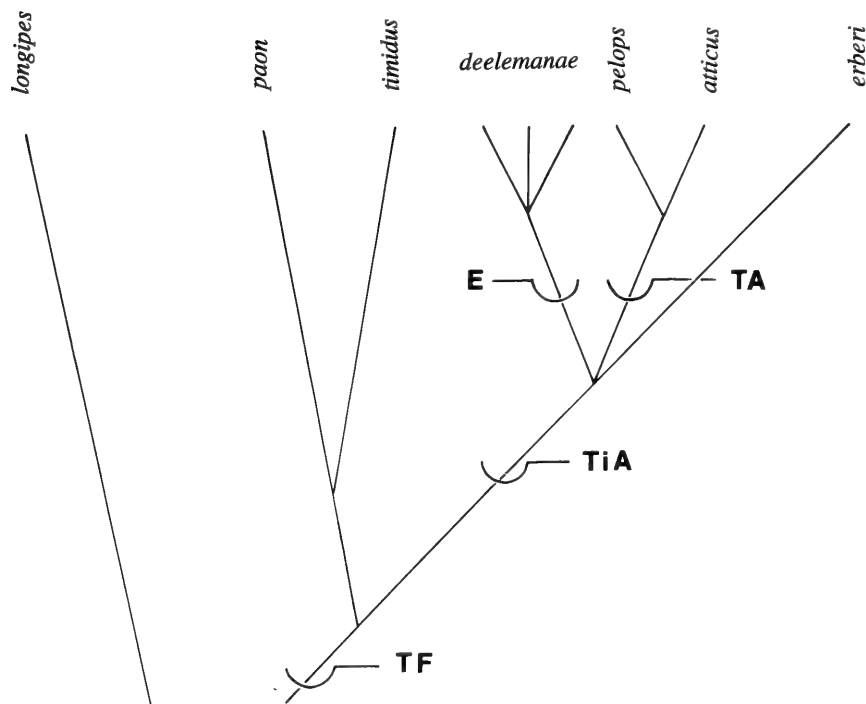


FIG. 53

Verwandschaftliche Beziehungen von *Amaurobius*-Arten in Peloponnes und Ägäis. Synapomorphien: Ausbildung von E Embolus, TA Tegularapophyse, TF Tegularfortsatz, TiA Tibialapophysen PA, MA, RA.

Exemplare von Kreta: Figs 11, 15, 23, 32, 50-51.

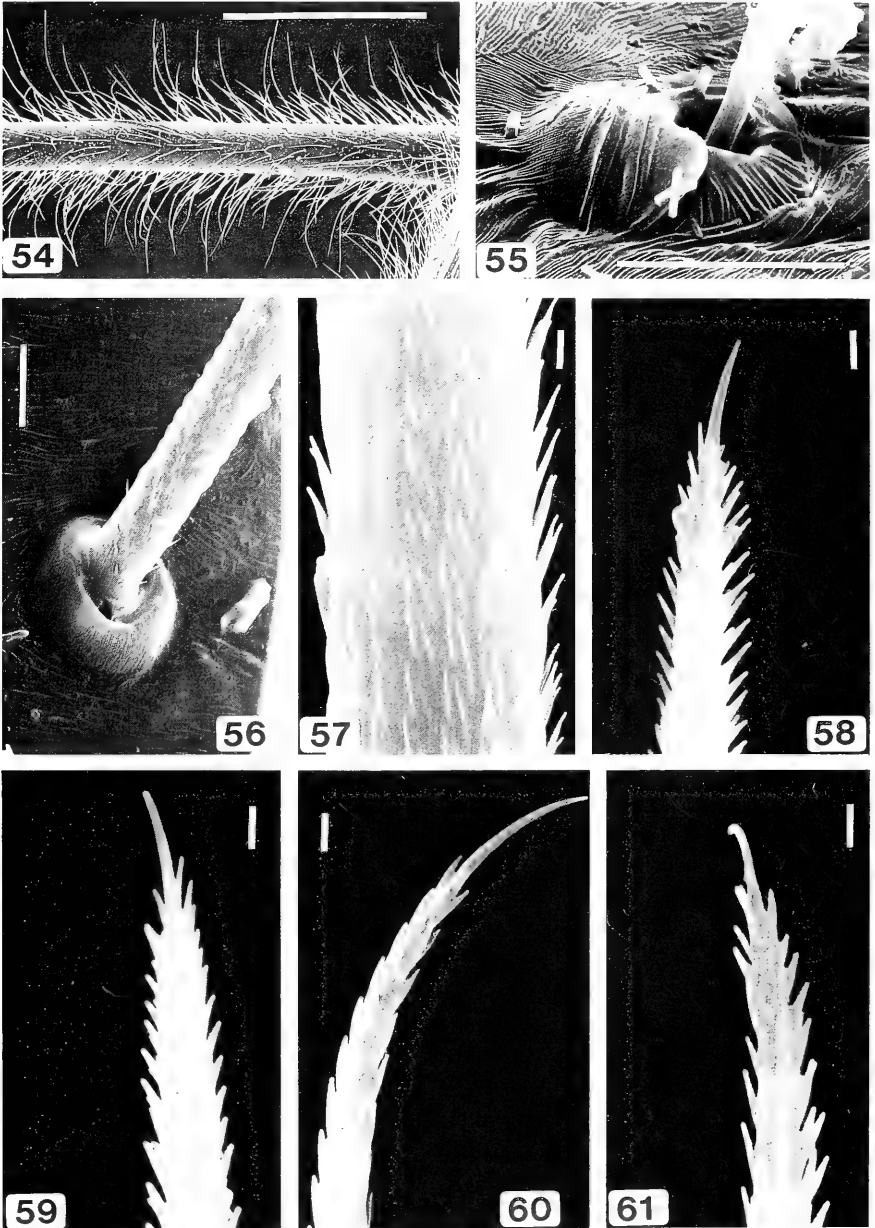
♂ ♀: Dimensionen [♂ (♀), mm]: Gesamtlänge 5.8 (6.0), Prosoma-Länge 3.1 (2.4, 2.7), Prosoma-Breite 2.1 (1.6, 2.1), Länge Femur I 3.2 (1.9), 1.03 (0.75) der Prosoma-Länge. Färbung und Zeichnung wie bei den Ex. von Naxos.

♂-Palpus: Apophysen der Tibia Figs 23, 32, Cymbium und Bulbus Figs 11, 15. PA kürzer, Nebenzahn der MA stärker, TF weniger stark als beim Holotypus.

Epigyne-Vulva: Figs 50, 51, Mittelplatte schmaler als beim ♀ von Naxos, die paramedianen Drüsengruben (?) des Epigaster wurden nicht beobachtet.

Exemplare von Rhodos: Figs 13, 16, 21, 30, 48-49.

♂ ♀: Dimensionen [♂ (♀), mm]: Gesamtlänge 5.2 (8.2), Prosoma-Länge 2.7 (3.0, 3.6), Prosoma-Breite 2.0 (2.0, 2.5), Länge Femur I 2.8 (2.2, 2.8), 1.0 (0.8) der Prosoma-Länge. Färbung und Zeichnung wie bei den übrigen Ex.



FIGS 54-61

Amaurobius longipes n. sp. (54, 56-59), *A. fenestralis* (Ström) (55, 61, Innsbruck, Martinswand, 20. Feber 1991), *A. jugorum* (L. Koch) (60, Nordtirol, Starkenbach, 21. April 1992). Absteheude Behaarung des ♂ Metatarsus I (54), Basis (56), Mitte (57) und Spitze (58-59) eines derartigen Haares. Haarspitze bei Vergleichsarten (60-61), Basis eines Becherhaares an Metatarsus IV (55). - Maßstäbe: 1.0 (54), 0.010 (55-56), 0.001 (57-61) mm.

♂-Palpus: Apophysen der Tibia Figs 21, 30, Cymbium und Bulbus Figs 13, 16. MA und Embolus wie beim Holotypus, PA distal abgeschrägt und fein zugespitzt, TF kürzer, seine Vorderwand steiler als beim Holotypus.

Epigyne-Vulva: Figs 48-49.

Amaurobius erberi (Keyserling, 1863)

Figs 2, 17, 27, 44-45

Fundort und Material: Chalkidike, Ag. Oros (Athos), Dafni, 1♂ 1♀ CTh, Ausobsky leg. 4. Mai 1969.

Die gut bekannte Art wird zum Vergleich abgebildet, Habitus ♂ Fig. 2. Rezente Charakterisierung noch bei LOKSA (1969), PESARINI (1991).

♂-Palpus: Apophysen der Taster-Tibia Figs 17, 27; RA weniger absteigend als bei den Vergleichsarten, MA ähnlich *A. deelemanae* n. sp., mit Nebenzahn, PA verlängert, distal abgewinkelt und zugespitzt. Cymbium und Bulbus Fig. 17, TF kurz, TA mit basaler Schuppe, Embolus gleichmäßig nach außen gekrümmt.

Epigyne-Vulva: Figs 44-45, auffällig die Gestalt der Rezeptakel.

Beziehungen: Der Tergularfortsatz von *A. erberi* ragt wie bei allen hier erwähnten Arten spitz vor. Nach der Konfiguration der Tibialapophysen bestehen nähere Beziehungen aber zu zwei von *A. erberi* durch je ein Sondermerkmal und das Verbreitungsgebiet getrennten Formengruppen: den *pelops*-Formen in NE-Peloponnes und Attika mit ihrer verlängerten Tergularapophyse und den durch Streckung des Embolus charakterisierten *deelemanae*-Formen der Ägäis.

Verbreitung: Locus typicus Insel Lesina = Hvar, Dalmatien. Die zahlreichen Fundangaben in BONNET (1955) suggerieren eine holomediterrane Verbreitung mit Randvorkommen auf der Iberischen Halbinsel, in Nordafrika, in der Ägäis, in Vorderasien und Südrussland. Eine Angabe von Kreta ist nach einem Jungtier und mit ? erfolgt (KULCZYNSKI 1903). Hier liegt *A. erberi* nur aus N-Griechenland vor, während in Peloponnes und Ägäis habituell ähnliche Formen nachgewiesen wurden. So sind die Verbreitungsgrenzen wohl neu zu bestimmen. In Italien ist *A. erberi* sehr häufig, nördlichste Vorkommen am Alpen-Südrand, bei Wien und in der Slowakei (THALER 1990, PESARINI 1991).

SCHLÜSSEL

Die neuen Arten fügen sich in die Bestimmungstabelle der ♂ der *Amaurobius*-Arten in SE-Europa (THALER & KNOFLACH 1993) wie folgt ein. Für 3 Arten des früheren Jugoslawien sind die ♂ noch immer nicht bekannt: *A. annulatus* Kulczynski, 1906 (Montenegro), *A. drensikii* Kratochvil, 1934 (Bosnien), *A. kratochvili* Miller, 1938 (Dalmatien, Insel Brac).

- 1 Palpen-Tibia mit 2 Apophysen *ferox*-Gruppe
(Zur Unterscheidung der Arten siehe PESARINI 1991)
- Palpen-Tibia mit 3 Apophysen: PA, MA, RA. 2
- 2 Vorderbeine stark verlängert, Femora I 1.5 mal so lang wie das Prosoma
. *A. longipes* n. sp. (Peloponnes: Parnon)

–	Vorderbeine kürzer, Femora I 1.0-1.2 der Prosoma-Länge	3
3	Tegularfortsatz TF nach ventrad/vorn abstehend	4
–	TF dem Bulbus eng anliegend	10
4	TF abgerundet	<i>A. hercegovinensis</i> Kylczynski, 1915 (Hercegovina)
–	TF zweigeteilt	<i>A. ossa</i> Thaler et Knoflach, 1993 (Thessalien)
–	TF triangulär	5
5	MA mit Nebenzahn	6
–	MA ohne Nebenzahn	9
6	Tegularapophyse TA verlängert, Figs 7-8	7
–	Tegularapophyse TA ohne Besonderheit, mit basaler Schuppe	8
7	Tibialapophysen wie Fig. 24	<i>A. pelops</i> Thaler et Knoflach, 1991 (NE-Peloponnes, Umgebung von Feneos; dort auch eine nahestehende Form noch unklaren Status, Fig. 25)
–	Tibialapophysen wie Fig. 26	<i>A. atticus</i> n. sp. (Attika)
8	Embolus gleichmäßig gekrümmt (Fig. 17), PA mit nach außen gekehrter Spitze (Fig. 20)	<i>A. erberi</i> (Keyserling, 1863)
–	Embolus länger, zunächst gerade nach vorn, dann nahezu rechtwinkelig nach außen verlaufend (Fig. 14), Tibialapophysen Fig. 22.	<i>A. deelemanae</i> n. sp. (Ägäis, Locus typicus Naxos) (Weitere Formen noch unklaren Status sind auf anderen Inseln der Ägäis zu erwarten; Exemplare von Kreta siehe Figs 15, 23, von Rhodos Figs 16, 21)
9	Tibialapophysen wie in Fig 19	<i>A. timidus</i> n. sp. (Peloponnes, Erimanthos)
–	Tibialapophysen siehe THALER & KNOFLACH (1993, Figs 7, 10)	<i>A. paon</i> Thaler et Knoflach, 1993 (Peloponnes, Taigetos)
–	Tibialapophysen siehe Thaler & Knoflach (1993, Figs 9, 12)	<i>A. pallidus</i> L. Koch, 1868 (SE-Europa)
10	Weitere Unterscheidungen wie in THALER & KNOFLACH (1993) <i>A. obustus</i> L. Koch, 1868 (expansiv bis SE-Alpen, Südtirol); <i>A. minor</i> Kulczynski, 1915 (Kroatien, Slovenien); <i>A. fenestralis</i> (Ström, 1768) (Europa, expansiv, nicht in Spanien)	

DISKUSSION UND ZUSAMMENFASSUNG

HABITAT, JAHRESZYKLUS: Die *Amaurobius*-Funde im Peloponnes stammen durchwegs aus den Tannenwäldern der Gebirge, Höhenlage ca. 900-1400 m, nicht aus dem küstennahen Tiefland. Habitatangaben für Attika und Ägäis lauten "unter *Platanus* bzw. Kiefern", zwei Funde gelangen in Höhlen, doch sind die betreffenden Formen höchstens als troglophil einzustufen. In ihrem jahreszeitlichen Auftreten stimmen mit einer Ausnahme alle Formen mit den Arten in Mitteleuropa überein: Zyklustyp diplochron, Reifehäutungen im Herbst und Überwinterung der Adulten. Lediglich *A. longipes* n. sp. weicht davon ab und erinnert an die Situation bei *Callobius claustrarius* (Hahn) in Mitteleuropa (stenochron-sommerreif, mit kurzlebigen ♂ und überwinternden ♀).

VERBREITUNG, BEZIEHUNGEN: Figs 52, 53. Uns haben aus Peloponnes und Ägäis bisher mindestens 5 Arten vorgelegen, jedoch keine der von BRISTOWE (1935) genannten Spezies (*A. erberi*, *A. pallidus* L. Koch, *A. scopoli* Thorell). Im Peloponnes verteilen sich die Formen auf die Gebirgsstöcke. Von dort ist bisher kein syntopisches Vorkommen bekannt, ein Zweifelsfall allerdings von Attika. Durch distinkte Merkmale gut unterscheidbare Formen sind in den Massiven des W- und S-Peloponnes beheimatet, Erimanthos (*A. timidus* n. sp.), Taigetos (*A. paon*), Parnon (*A. longipes* n. sp.). In NE-Peloponnes und Attika (*A. pelops*, *A. atticus* n. sp.) bzw. auf Inseln der Ägäis (*A. deelemanae* n. sp.) treten dagegen zwei polytypische Komplexe auf, deren Untergliederung und Abgrenzung noch weiter untersucht werden sollte. Die taxonomische Anerkennung schien uns vorerst weder für die Formen von *A. deelemanae* n. sp. auf Rhodos und Kreta sinnvoll, noch für eine weitere *pelops*-Form aus der Umrandung des Feneos-Beckens. Das vikariante Auftreten der *Amaurobius*-Arten in Peloponnes und Ägäis ist ein nachdrücklicher Hinweis auf Speziation als Folge von Areal-Disjunktionen und Isolation.

Fig. 53 zeigt unsere Vorstellungen über die verwandtschaftlichen Zusammenhänge. Der mediterran-expansive *A. erberi* bildet zusammen mit den polytypischen Komplexen um *A. pelops* in NE-Peloponnes und Attika und mit den *A. deelemanae*-Formen der Ägäis eine durch die Tibialapophysen charakterisierte Gruppe, die in der Ausbildung des Tegularfortsatzes mit den markanten Gebirgsarten in Erimanthos (*A. timidus* n. sp.) und Taigetos (*A. paon*) übereinstimmt. *A. longipes* n. sp. aus dem Parnon nimmt morphologisch und biologisch eine Sonderstellung ein.

GESCHLECHTSDIMORPHISMUS: Figs 54-61. Die Vorderbeine der ♂ von *A. longipes* n. sp. weisen wie die anderer *Amaurobius*-Arten eine auffällige Behaarung aus allseitig lang abstehenden Haaren auf, Fig. 54. Die zarten Einzelhaare wurzeln anders als ein Trichobothrium (Fig. 55) in einem glatten, eng anliegenden Sockel (Fig. 56) und scheinen also dem "closed tactile hair" bei HARRIS & MILL (1977) zu entsprechen. Haarschaft fein gefiedert (Fig. 57) und wie bei zwei Vergleichsarten (Figs 60-61) in eine feine Spitze ausgezogen (Figs 58-59).

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Les Scorpions (Chelicerata, Scorpiones) de l'Equateur avec quelques considérations sur la biogéographie et la diversité des espèces

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The scorpions (Chelicerata, Scorpiones) from Ecuador, with some considerations on biography and diversity of species. - The scorpion-fauna of Ecuador has been intensively studied in the last 15 years, but this paper represents the first attempt to produce a framework contribution to this fauna. Four families are present: Bothriuridae, Buthidae, Chactidae and Iuridae, with 8 genera and 36 species. Predominant distributional patterns show an Amazonian origin for some Buthidae (genus *Ananteris* and *Tityus*) and Chactidae (genus *Chactas*), whereas several other Buthidae (genus *Tityus*, Chactidae (genus *Teuthraustes*) and Iuridae (genus *Hadruioides*) represent a typical andine fauna. Bothriuridae genus *Brachistosternus* has affinities with a meridional South American fauna whereas Buthidae genus *Centruroides* has affinities with Central America. Scorpion biogeographic patterns observed in the natural regions of Ecuador correspond closely with those proposed by HAFFER (1990) and Gentry (1992) and complement previous conclusions regarding scorpion biogeography.

Key-words: Scorpion - Ecuador - Biogeography - Biodiversity.

INTRODUCTION

L'Equateur compte parmi les régions du monde les mieux étudiées en ce qui concerne la faune scorpionique. Ainsi, dès le 19ème siècle de nombreux travaux ont été publiés dont la majorité décrivait de nouveaux taxa (GERVAIS, 1844; POCKOCK, 1893, 1898; BORELLI, 1899). C'est KRAEPELIN (1912) qui proposa la première synthèse des diverses études sur les espèces de la sous-famille des Chactinae comprenant les *Teuthraustes* de l'Equateur. D'autres travaux ponctuels ont suivi (MEISE, 1934), mais c'est avec la monographie de MELLO-LEITÃO (1945), sur les Scorpions sud-américains, que l'ensemble de la faune équatorienne connue à l'époque est traitée.

* Manuscrit accepté le 14.04.1994.

Ensuite il faut attendre près de trente ans avant que l'on s'intéresse aux Scorpions de l'Equateur. KINZELBACH (1973) traite de la faune des îles Galapagos tandis que d'autres auteurs, lors de révisions de certains groupes, touchent à des espèces équatoriennes (MAURY, 1974; FRANCKE, 1977).

Dans les années quatre-vingts plusieurs nouvelles études contribuent à un élargissement des connaissances sur les Scorpions équatoriens (LOURENÇO, 1980, 1981, 1982B, 1983, 1984A, B, 1986A, B, 1988A, B; LOURENÇO & MAURY, 1985; MAURY & LOURENÇO, 1987; SISSOM & LOURENÇO, 1987).

L'opportunité de cette présente synopsis se justifie en raison de la nette progression des connaissances sur les modèles de distribution et de différenciation des Scorpions, ainsi que sur la délimitation des centres d'endémisme, non seulement en Equateur, mais aussi dans les pays limitrophes tels la Colombie, le Pérou, le Brésil et le Venezuela (LOURENÇO, 1994a, b, c, sous presse, A, B). En outre, l'étude des collections équatoriennes déposées à l'Université catholique de Quito (UCQ) et au Muséum de Genève (MHNG) a permis de clarifier divers points obscurs encore existants dans la systématique de diverses espèces.

MATÉRIEL ET MÉTHODES

L'importance des collections déposées à l'Université catholique de Quito et au Muséum d'histoire naturelle de Genève a stimulé notre intérêt et fourni l'ossature de la présente étude (cf. LOURENÇO 1988A). En outre, les missions effectuées par l'auteur en Colombie depuis 1988, ont contribué à une meilleure connaissance de la faune scorpionique régionale et des caractéristiques biogéographiques et écologiques des régions andines.

Le traitement taxonomique utilisé dans ce travail est applicable uniquement à l'Equateur et aux régions voisines (i.e. Amazonie occidentale, sud de la Colombie et Choco et nord du Pérou). Pour les nouvelles espèces, des descriptions complètes mais sommaires sont apportées. Pour les espèces du genre *Teuthraustes*, très homogènes, seuls les caractères différenciels sont illustrés dans de courtes diagnoses. Des descriptions longues mais peu précises existent déjà dans la littérature classique (KRAEPELIN 1912; MELLO-LEITÃO 1945).

Les mesures, obtenues avec un grossissement de 6,4 x, sont données en millimètres. La terminologie utilisée est celle proposée par STAHNKE (1970), complétée par celles de VACHON (1963, 1974, 1975).

LISTE DES SCORPIONS SIGNALÉS EN L'EQUATEUR

Les taxa de même rang sont indiqués par ordre alphabétique et leur traitement dans le texte suit la même séquence.

Famille des Bothriuridae Simon, 1880.

Genre *Brachistosternus* Pocock, 1894.

Brachistosternus (B) ehrenbergi (Gervais, 1841).

Famille des Buthidae Simon, 1880.

Genre *Ananteris* Thorell, 1891.

Ananteris ashmolei Lourenço, 1981.

Ananteris festae Borelli, 1899.

Genre *Centruroides* Marx, 1889.

Centruroides exsul (Meise, 1934).

Centruroides gracilis (Latreille, 1804).

Centruroides margaritatus (Gervais, 1841).

Genre *Tityus* Koch, 1836.

Tityus asthenes Pocock, 1893.

Tityus bastosi Lourenço, 1984.

Tityus demangei Lourenço, 1981.

Tityus ecuadorensis Kraepelin, 1896.

Tityus forcipula (Gervais, 1844).

Tityus gasci Lourenço, 1981.

Tityus intermedius Borelli, 1899.

Tityus jussarae Lourenço, 1988.

Tityus pugilator Pocock, 1898.

Tityus roigi Maury et Lourenço, 1987.

Tityus silvestris Pocock, 1897.

Tityus simonsi Pocock, 1900.

Famille des Chactidae Laurie, 1896.

Genre *Chactas* Gervais, 1844.

Chactas camposi Gervais, 1844.

Chactas mahnerti, nouvelle espèce.

Genre *Teuthraustes* Simon, 1878.

Teuthraustes atramentarius Simon, 1878.

Teuthraustes dubius (Borelli, 1899).

Teuthraustes festae (Borelli, 1899).

Teuthraustes gervaisi (Pocock, 1893).

Teuthraustes lojanus (Pocock, 1900).

Teuthraustes oculatus (Pocock, 1900).

Teuthraustes ohausi Kraepelin, 1912.

Teuthraustes rosenbergi (Pocock, 1898).

Teuthraustes simonsi (Pocock, 1900).

Teuthraustes whymeri (Pocock, 1893).

Teuthraustes witti Kraepelin, 1896.

Genre *Troglotayosicus* Lourenço, 1981.

Troglotayosicus vachoni Lourenço, 1981.

Famille des Iuridae Thorell, 1876.

Genre *Hadruioides* Pocock, 1893.

Hadruioides galapagoensis Maury, 1974.

Hadruioides leopardus Pocock, 1900.
Hadruioides maculatus (Thorell, 1876).
Hadruioides udvardyi nouvelle espèce.

Famille des BOTHRIURIDAE Simon, 1880.

Genre **Brachistosternus** Pocock.

1. **Brachistosternus (B.) ehrenbergi** (Gervais, 1841).

Cette espèce est la seule du genre à être citée de l'Equateur. Décrite du Pérou, elle a été ensuite signalée en Equateur, Colombie et Panama (MAURY, 1973). Au cours de missions récentes en Colombie, aucun spécimen appartenant à cette espèce n'a été retrouvé (LOURENÇO & FLOREZ 1990A, B), et sa présence dans ce pays et au Panama semble peu probable. Elle pourrait néanmoins exister dans des zones arides de l'Equateur. De nouvelles collectes devront répondre à cette question. Au cours de la présente étude aucun matériel appartenant à l'espèce n'a été examiné.

Famille des BUTHIDAE Simon, 1880.

Genre **Ananteris** Thorell.

1. **Ananteris ashmolei** Lourenço, 1981.

Décrite de la Province de Morona-Santiago, cette espèce demeure un endémique pour cette région de l'Equateur. En effet, sa répartition antérieurement supposée en Colombie, Panama et Costa Rica a été restreinte par la suite (LOURENÇO 1991, 1993). Au cours de la présente étude aucun matériel supplémentaire n'a été examiné.

2. **Ananteris festae** Borelli, 1899.

Cette ancienne espèce décrite de l'Equateur par BORELLI, était restée peu connue jusqu'à la révision de LOURENÇO (1982B). L'étude d'un matériel supplémentaire nous autorise à la définir comme un élément endémique de l'Equateur et plus précisément du centre d'endémisme Chimborazo (LOURENÇO 1988B; BROWN 1979). Aucun exemplaire supplémentaire n'a été examiné au cours de la présente étude (LOURENÇO 1988A).

Genre **Centruroides** Marx, 1889.

Trois espèces appartenant à ce genre ont été signalées pour l'Equateur: *Centruroides gracilis* (Latreille, 1804), *Centruroides margaritatus* (Gervais, 1841) et *Centruroides exsul* (Meise, 1934).

Pour *Centruroides gracilis* les citations d'Equateur sont anciennes et demandent confirmation; cependant sa présence dans les zones arides de la côte pacifique est tout à fait vraisemblable (SISSOM & LOURENÇO 1987; LOURENÇO & FLOREZ 1990A, B).

Centruroides margaritatus (Figs 1 et 2) a été décrite de la Isla de Puna en Equateur, et depuis, sa distribution a été considérablement élargie sur l'Amérique du Sud (Colombie, Ecuador, Venezuela), l'Amérique centrale, jusqu'au Mexique et sur diverses îles de la région Caraïbes.

Centruroides exsul est une espèce endémique des îles Galapagos (MEISE 1934; KINZELBACH 1973). Un traitement taxonomique assez détaillé des trois espèces est proposé par SISSOM & LOURENÇO (1987). Aucun matériel supplémentaire n'a été examiné au cours de la présente étude.



FIGS 1-2

Centruroides margaritatus, vue dorsale. 1. Mâle. 2. Femelle (holotype) de l'île de Puna, Equateur.

Genre **Tityus** Koch, 1836.

Au total 12 espèces appartenant à ce genre très divers et difficile et qui en comporte plus d'une centaine, ont été citées et confirmées pour l'Equateur. A la suite de la monographie de MELLO-LEITÃO (1945), diverses contributions ont mieux redéfini la faune de *Tityus* de l'Equateur (LOURENÇO 1981, 1984A, B, 1988A; LOURENÇO & MAURY 1985).

Les douze espèces équatoriennes de *Tityus* peuvent être associées à des groupes naturels distincts, mais encore peu précisément définis à l'heure actuelle. Ainsi, le découpage proposé ici doit être considéré comme provisoire.

1. Groupe **Tityus clathratus**, Koch, 1845.

Espèces présentes en Equateur: *Tityus bastosi* Lourenço, 1984, *Tityus intermedius* Borelli, 1899, *Tityus silvestris* Pocock, 1897.

Tityus intermedius (Figs 3 et 4) apparaît comme une espèce propre à la région andine au nord de l'Equateur et au sud de la Colombie. *Tityus bastosi* et *Tityus silvestris* sont des espèces à large répartition amazonienne. Ces deux espèces présentent des caractéristiques polymorphes définies comme "ochlospecies" (LOURENÇO 1988C). L'ensemble du groupe *Tityus clathratus* est analysé par Lourenço (1984A, 1992), accompagné de considérations biogéographiques.

2. Groupe de **Tityus bolivianus** Kraepelin, 1894.

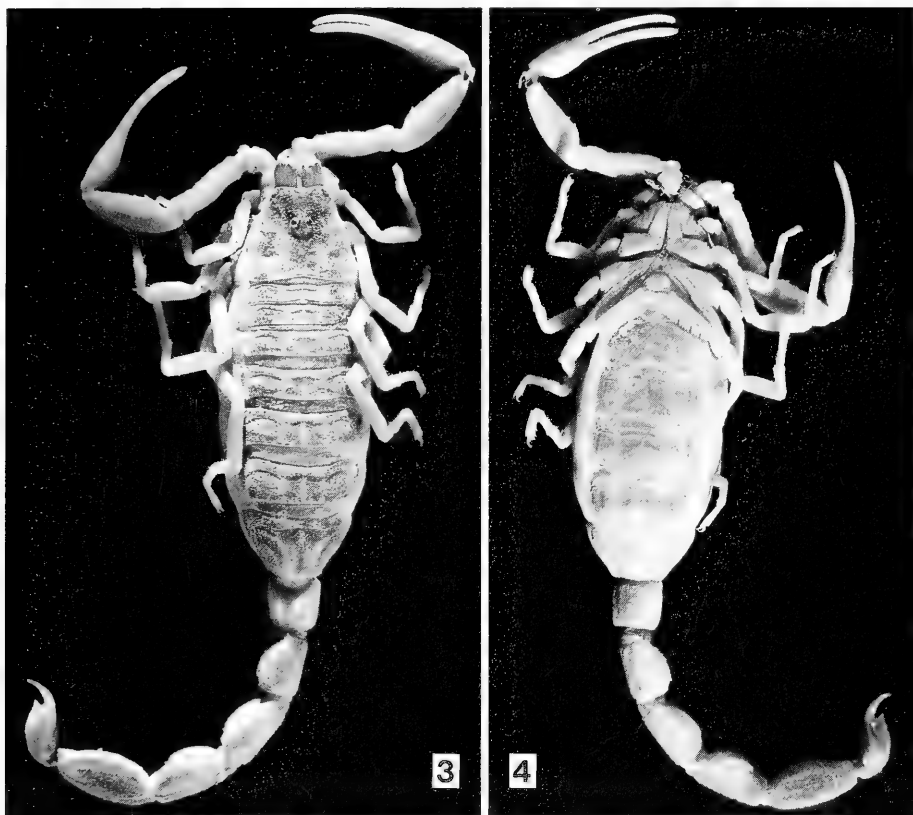
Défini par MELLO-LEITÃO (1945), ce groupe a été revu par Lourenço & Maury (1985). L'actuelle diagnose pourra être modifiée selon des critères réductionnistes ou divisionnistes.

Espèces présentes en Equateur: *Tityus demangei* Lourenço, 1981, *Tityus ecuadorensis* Kraepelin, 1895, *Tityus jussarae* Lourenço, 1988, *Tityus pugilator* Pocock, 1898, *Tityus roigi* Maury et Lourenço, 1987, *Tityus simonsi* Pocock, 1900.

Les différentes espèces de ce groupe retrouvées en Equateur se caractérisent par leur distribution typiquement andine, sur le Plateau Central. *T. demangei*, *T. jussarae*, *T. pugilator* et *T. roigi* peuvent être considérées jusqu'à présent comme endémiques équatoriennes. *Tityus ecuadorensis* et *T. simonsi* ont également une répartition andine péruvienne. Une analyse taxonomique assez détaillée est présentée apportée par LOURENÇO & MAURY (1985).

3. Groupe **Tityus asthenes** Pocock, 1893.

Au sein de ce groupe constitué d'espèces de couleur sombre et de grande taille, seule *Tityus asthenes* définissant le groupe, est retrouvée en Equateur. Cette espèce est propre aux forêts humides. En Equateur elle présente une distribution disjointe sur les deux versants andins; dans la région amazonienne à l'est (Province Napo), et dans les forêts de la côte pacifique à l'ouest (Province Esmeraldas).



FIGS 3-4

Tityus intermedius (holotype-femelle), vues dorsale et ventrale.

Tityus asthenes se rencontre de l'Amazonie équatorienne jusqu'à Panama et au Costa Rica. Les populations locales présentent des différences morphologiques d'ordre essentiellement morphométrique. Il en est ainsi des deux populations équatoriennes.

4. Groupe *Tityus forcipula* (Gervais, 1844).

Le groupe *Tityus forcipula* déjà bien défini par LOURENÇO (1984B) comporte des espèces caractérisées par une grande taille et une spinulation très importante. Comme pour le groupe précédent, seule l'espèce définissant le groupe (*T. forcipula*) est présente en Equateur, où elle est distribuée sur le Plateau central, dans les régions du centre et du nord, à des altitudes allant de 1500 à 2000 mètres.

Actuellement deux espèces très voisines de *Tityus forcipula* (i.e. *Tityus spinatus* Pocock et *Tityus cuellari* Lourenço), font l'objet d'une étude comparative détaillée dans le but de redéfinir correctement le statut de ces trois espèces. Nous devons considérer ces deux dernières soit en tant que simples variétés de *T. forcipula*, soit les valider comme espèces très voisines, mais distinctes (cf. *T. spinatus* a été mis en synonymie de *T. forcipula*; LOURENÇO 1984B).

5. Groupe **Tityus melanostictus** Pocock, 1893.

Le groupe *Tityus melanostictus*, caractérisé par des espèces de couleur jaunâtre très clair, de taille moyenne, a été assez bien redéfini par LOURENÇO & EICKSTEDT (1987).

Une seule espèce appartenant à ce groupe, *Tityus gasci* Lourenço, 1981, est présente en Equateur. Décrite à l'origine de la Guyane française, elle a été retrouvée par la suite dans de nombreuses stations sur l'ensemble de la région amazonienne. Sa présence en Amazonie équatorienne (Napo), correspond en quelque sorte à la limite occidentale de sa distribution. Cette espèce ainsi que *T. bastosi* et *T. silvestris* (groupe *T. clathratus*), présente des caractéristiques d'espèce polymorphe du type "ochlo-species".

Famille des CHACTIDAE Laurie, 1896.

Genre **Chactas** Gervais, 1844.

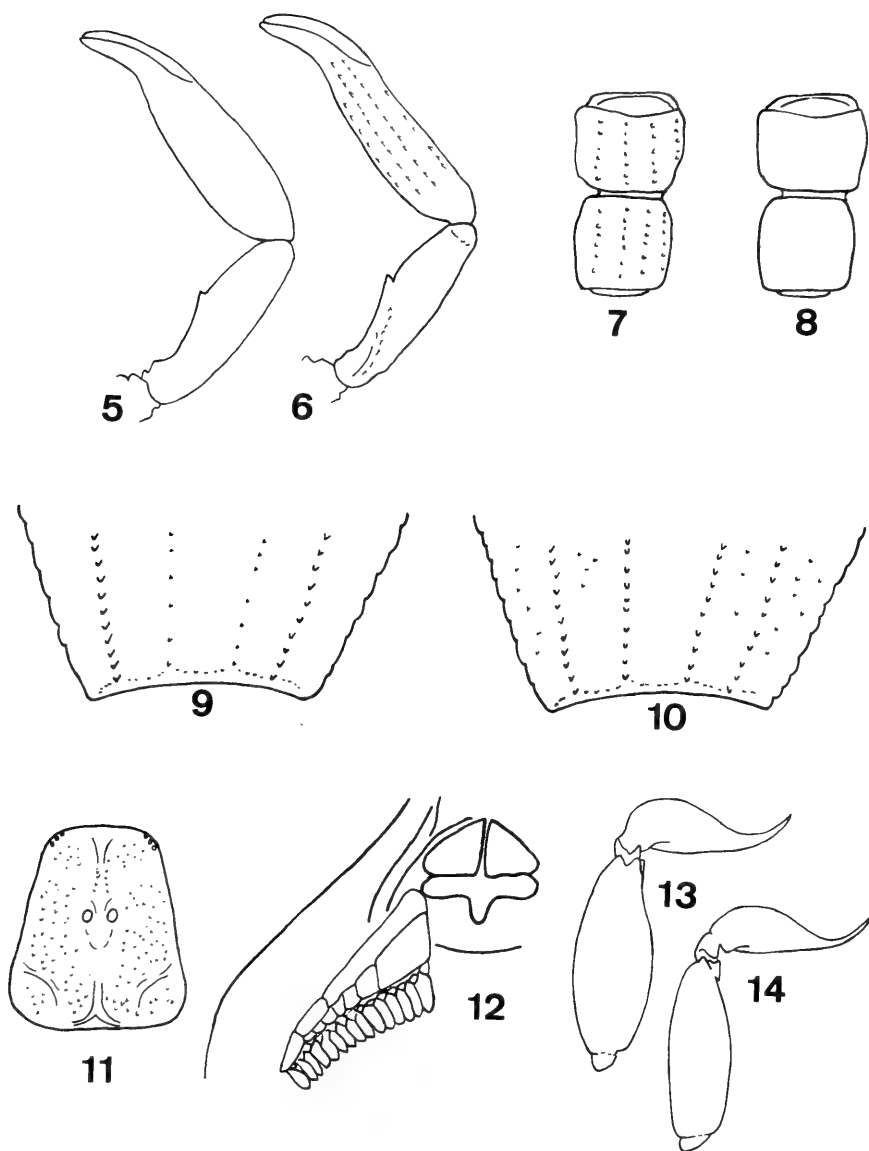
Jusqu'au travail de MELLO-LEITÃO (1945), une seule espèce appartenant à ce genre, était connue pour l'Equateur. *Chactas camposi* Mello-Leitão, 1939 a été décrite de Guaiquil en Equateur, et demeure très mal connue jusqu'à présent. Une description insuffisante, associée à la perte quasi certaine du type, empêche de statuer sur sa valeur taxonomique. Au cours de la présente étude aucun matériel correspondant à cette espèce n'a été examiné. Seule l'étude d'un matériel topotype pourra justifier une validation de *Chactas camposi*.

L'examen de trois exemplaires d'une autre espèce de *Chactas* nous a amené à décrire une espèce nouvelle; cependant, avant cette description, quelques considérations sur *Chactas vanbenedeni* et l'espèce nouvelle nous semblent nécessaires.

Chactas vabenedeni a été décrite de Colombie, sans précision de localité. Le type de Gervais est sans aucun doute perdu, ce qui empêche toute vérification sur la réelle identité de cette espèce.

Plusieurs autres espèces de *Chactas* de Colombie et du Venezuela possèdent des caractéristiques voisines de celles de *C. vanbenedeni*. Ainsi certains auteurs tel MELLO-LEITÃO (1945) ont cité cette espèce de diverses localités colombiennes (e.g. Muzo) lesquelles sont certainement erronées.

Chactas fuchsii Berthold, 1846 a été décrite de Popayan au sud de la Colombie, et a été mise par la suite en synonymie de *C. vanbenedeni*. A partir des travaux de



FIGS 5-14

5-6: Tibias et pinces, vue dorsale. 5. *Chactas mahnerti* (holotype-mâle). 6. *Chactas vanbenedeni* de Colombie); 7-8: Ier et IIème anneaux du metasoma, vue ventrale. 7. *Teuthraustes* du groupe I, avec carènes. 8. *Teuthraustes* du groupe II, sans carènes (cf. fig. 29); 9-10: Vème sternite, vue ventrale. 9. *Hadruioides udvardyi* (holotype-mâle). 10. *Hadruioides carinatus* (mâle); 11-12: *Hadruioides udvardyi* (holotype-mâle). 11. Plaque prosomienne. 12. Opercule génital et peigne; 13-14. *Hadruioides udvardyi* Vème anneau du metasoma et telson, vue latérale. 13. Allotype-femelle. 14. Holotype-mâle.

LOURENÇO & FLOREZ (1990A, B) sur les Scorpions de la région pacifique de Colombie, *C. vanbenedeni* a été définitivement associée à la forme trouvée sur la côte sud pacifique de Colombie. De plus elle est considérée comme différente des formes du groupe *Chactas lepturus* (e.g. *C. lepturus* Thorell, *C. keyserlingi* Pocock), distribuées sur la cordillère orientale de Colombie (Lourenço, 1991). GONZALEZ-SPONGA (1984) cite *C. vanbenedeni* pour le Venezuela sans aucune précision de station. Cette indication est certainement incorrecte.

Les caractéristiques morphologiques de *C. vanbenedeni* prêtent aussi à confusions. Ainsi les valeurs morphométriques citées par MELLO-LEITÃO (1945) diffèrent de celles données par Pocock (1893). En outre, la coloration décrite par MELLO-LEITÃO (1945) diverge de celle donnée par KRAEPELIN (1894).

Deux décisions sont prises ici: - a. Assigner définitivement la forme de la région sud-pacifique de Colombie à *C. vanbenederi*. - b. Décrire la forme retrouvée en Equateur en tant qu'espèce nouvelle, associée à *C. vanbenedeni*.

Chactas mahnerti n. sp.

Holotype (♂): Equateur, Prov. Pichincha, San Antonio, 20/I/1985 (M. Julloa) (MHNG).

Paratypes: 1 ♂ adulte, Equateur: Prov. Pichincha, La Florida (cerca Alluriquin), 15/IX/1984 (L. Coloma) (Bajo la corteza de un arbol) (UCQ). 1 immature, Equateur, Prov. Napo, Coca, III/1986 (G. Onore) (MHNG).

E t y m o l o g i e : Le nom spécifique est attribué en hommage au Dr. V. Mahnert, Directeur du Muséum d'histoire naturelle de Genève.

D i a g n o s e : Espèce associée à *Chactas vanbenedeni* (Gervais), mais caractérisée par une coloration rougeâtre du corps et ocre-jaune des pattes, tandis que la coloration de *C. vanbenedeni* est plus foncée, globalement brunâtre. Pédipalpes et particulièrement les pinces très lisses et brillantes chez la nouvelle espèce (Fig. 5); chez *C. vanbenedeni* la pince présente des carènes et une sculpture plus carrée (Fig. 6). Les valeurs morphométriques comparatives sont indiquées dans le tableau I.

D e s c r i p t i o n fondée sur l'holotype mâle et un paratype mâle (adultes).

Coloration générale rougeâtre; Prosoma et Mésosoma plus foncés rouge-noirâtre. Tubercule oculaire et yeux latéraux noirâtres. Sternites jaune-rougeâtre; quatrième et cinquième plus foncées. Métasoma: anneaux I à V rougeâtres. Telson plus claire, rouge-jaunâtre; aiguillon rougeâtre. Peignes et opercule-génital jaune-clair. Sternum et hanches jaune-rougeâtre. Processus maxillaires rougeâtre foncé. Pattes ocre-jaune; pédipalpes rougeâtres avec des tons noirâtres; la pince plus claire; doigts des pinces noirâtres. Chélicères jaunâtres avec une trame rougeâtre-foncée dans la partie antérieure; les doigts sont rougeâtre foncé.

M o r p h o l o g i e

Prosoma: Plaque prosomienne avec le front légèrement convexe, presque droit. Tubercule oculaire antérieur par rapport au centre de la plaque prosomienne. Yeux

médians séparés par moins d'un diamètre oculaire. Deux paires d'yeux latéraux. Pas de granulation sur la surface de la plaque prosomienne; chagrinée;

Mesosoma: Tergites sans carènes; pas de granulations; chagrinés également.

Métasoma: Anneaux I et II sans carènes; III à V avec quelques esquisses de carènes. Carènes dorsales du IV et V anneaux plus marquées. Carènes ventrales du V anneau avec quelques granules spiniformes. Espaces intercarénaux des anneaux I à III non granulés. Vésicule à face dorsale lisse et à faces latérales et ventrales faiblement granulées. Sternites à stigmates arrondis. Peignes avec 8-8 dents (paratypes avec 8-8 et 7-7).

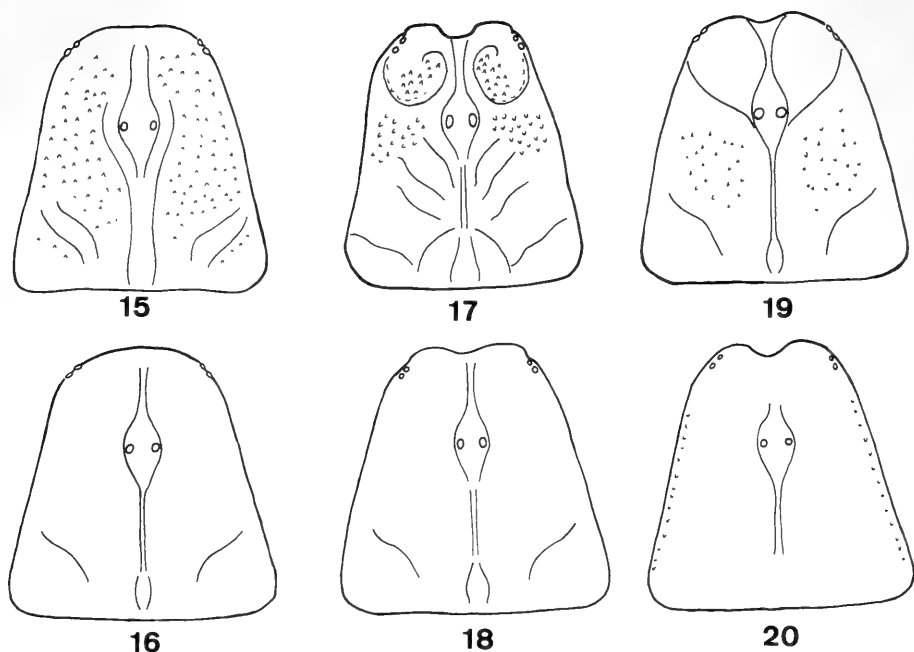
Pédipalpes: Fémur avec 5 carènes presque toutes complètes; Tibia avec des esquisses de carènes; Pince lisse sans carènes; face interne du Fémur et du Tibia avec quelques granules spiniformes. Tous les segments très faiblement granulés, à tégument chagrinés. Tarsomère II de toutes les pattes avec une série médiano ventralo longitudinale de 3 à 4 épines aiguës en forme de soie. Chélicères avec la densition caractéristique des Chactidae. Trichobothriotaxie: Néobothriotaxie type C, avec présence de 5 trichobothries sur la face ventrale du Tibia. Caractère diagnostique du genre.

Genre *Teuthraustes* Simon, 1878

Depuis la création du genre *Teuthraustes* par SIMON (1878) et jusqu'à sa révision par KRAEPELIN (1912), treize espèces ont été décrites ou transférées dans ce genre. A l'exception de deux espèces; *Teuthraustes amazonicus* Simon et *Teuthraustes glaber* Kraepelin, du Pérou, les onze restantes ont été décrites de l'Equateur. Cette importante concentration des espèces de *Teuthraustes* en Equateur, même si elle peut soulever des doutes sur le statut de certaines d'entre elles, est vraisemblable et peut être expliquée par un modèle déjà proposé par GENTRY (1992) pour des plantes du genre *Gasteranthus*, réparties dans la même région de distribution que les *Teuthraustes*. Selon GENTRY le processus opérateur semble être associé à une sorte de dérive génétique dans de petites populations fondatrices; un processus similaire à celui postulé pour les *Drosophiles* hawaïennes (LOURENÇO, 1994c, sous presse b).

Jusqu'au travail de MELLO-LEITÃO (1945) aucune espèce nouvelle n'a été ajoutée à ce genre. Par la suite deux espèces ont été décrites du Venezuela: *Teuthraustes carmelinae* Scorza, 1954 et *Teuthraustes adrianae* Gonzalez-Sponga, 1975. Une du Brésil: *Teuthraustes lisei* Lourenço, 1994, et une de la Colombie: *Teuthraustes guerdouxi* Lourenço, 1994.

Dans la présente étude sur les Scorpions de l'Equateur, la grande majorité du matériel examiné appartenait au genre *Teuthraustes*. Quatre espèces ont été identifiées. En s'appuyant sur l'important matériel de Genève et de Quito, ainsi que sur l'examen d'une majorité des types, il nous a paru possible d'apporter quelques compléments d'information taxonomiques servant à faciliter l'identification des espèces équatoriennes de ce genre très homogène et difficile. La révision de KRAEPELIN (1912), reprise par MELLO-LEITÃO (1945) apporte peu de clarification. Les clés d'identification proposées par ces deux auteurs sont d'une utilisation difficile et peuvent induire des erreurs. Dans



FIGS 15-20

Plaques prosomiennes (mâles). 15. *Teuthraustes atramentarius*. 16. *Teuthraustes oculatus*. 17. *Teuthraustes whymperi*. 18. *Teuthraustes witti*. 19. *Teuthraustes ohausi*. 20. *Teuthraustes gervaisi*.

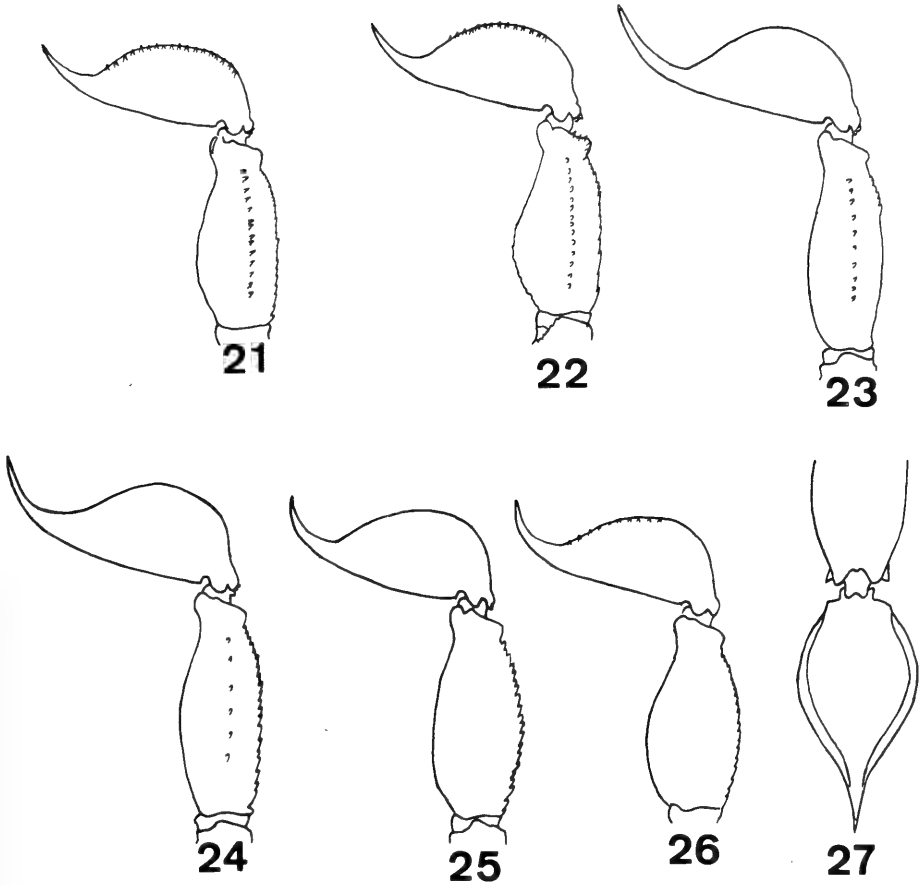
la mesure du possible, nous tâcherons d'indiquer ici des caractères facilement repérables pour l'identification de quelques espèces. La distribution géographique des espèces de *Teuthraustes* est en général limitée à des aires très précises et peut ainsi constituer un facteur important dans la définition des populations.

Premier groupe: *Teuthraustes atramentarius* Simon et *Teuthraustes oculatus* Pocock.

Ces deux espèces peuvent être distinguées de leurs congénères par la présence de carènes ventrales et latéro-ventrales sur les anneaux I et II du Métasoma (Fig. 7). *Teuthraustes atramentarius* et *T. oculatus* peuvent être différenciées d'après la structure de la plaque prosomienne: convexe, très granulée et bossue chez *T. atramentarius*; lisse et chagrinée chez *O. oculatus* (Figs 15 et 16).

Les deux espèces habitent le Plateau central du nord de l'Equateur. Dans les Provinces de Pichincha et Imbabura pour *T. atramentarius* et dans la Province de Cotopaxi pour *T. oculatus*.

Teuthraustes atramentarius est l'espèce la plus commune du genre avec des populations très abondantes en Equateur.



FIGS 21-27

Vème anneau du metasoma et telson, vue latérale. 21. *Teuthraustes atramentarius*. 22. *Teuthraustes oculatus*. 23. *Teuthraustes whymperi*. 24. *Teuthraustes witti*. 25. *Teuthraustes ohausi*. 26. *Teuthraustes gervaisi*. 27. Idem, vue dorsale.

Deuxième groupe: *Teuthraustes dubius* Borelli, *Teuthraustes festae* Borelli, *Teuthraustes gervaisi* Pocock, *Teuthraustes lojanus* Pocock, *Teuthraustes ohausi* Kraepelin, *Teuthraustes rosenbergi* Pocock, *Teuthraustes simonsi* Pocock, *Teuthraustes whymperi* Pocock et *Teuthraustes witti* Kraepelin.

Les espèces de ce groupe sont caractérisées par l'absence de carènes ventrales et latéro-ventrales sur les anneaux I et II du Metasoma (Figs 8 et 29).

Dans l'ensemble du matériel étudié ici nous avons identifié *Teuthraustes whymperi* et *Teuthraustes witti* parmi les espèces du deuxième groupe.

Teuthraustes whymperi est de toute évidence très commune à Las Pampas, Province Cotopaxi. Elle peut être facilement identifiée par la présence d'une plaque

prosomienne concave, granulée et par un telson lisse, avec un aiguillon très long et peu incurvé (Figs 17 et 23). *Teuthraustes witti* apparaît comme une espèce voisine mais se caractérise par la présence d'une plaque prosomienne concave beaucoup plus lisse que celle de *T. whymperi*. Le telson de *T. witti* est plus robuste et moins long que celui de *T. whymperi* et la face ventrale du Vème anneau du Métasoma est plus granulée (Figs 18 et 24).

Pour les quatre espèces identifiées dans le matériel de Quito et du Muséum de Genève les types ont été étudiés. Pour les autres espèces, les types, mais aussi quelques exemplaires non-types ont été examinés, autorisant les conclusions suivantes:

Teuthraustes dubius et *Teuthraustes festae*, toutes les deux décrites de la vallée du Rio Santiago dans la Province de Morona-Santiago, sont de toute évidence endémiques pour cette région (LOURENÇO, 1981).

Teuthraustes dubius est voisine de *Teuthraustes amazonicus*, espèce décrite de Pebas en Amazonie péruvienne, tandis que *Teuthraustes festae* est proche de *T. witti*. Ces deux espèces sympatriques peuvent être facilement distinguées par la forme de leur telson; large robuste et granulé chez *T. festae*; lisse et fin chez *T. dubius* (Figs 28 à 30).

L'étude des types de *T. gervaisi*, *T. lojanus*, *T. rosenbergi*, *T. simonsi* et *T. ohausi*, autorise à considérer ces espèces comme valables, à l'exception peut-être de *T. lojanus*, qui pourrait correspondre à une simple variété de *T. witti*. A observer que ces deux espèces sont sympatriques dans la Province de Loja. La décision de placer *T. lojanus* dans la synonymie de *T. witti* demeure cependant difficile sur la base de la seule étude de types de *T. lojanus*. Seules des collectes d'un matériel topotype pourront résoudre cette question.

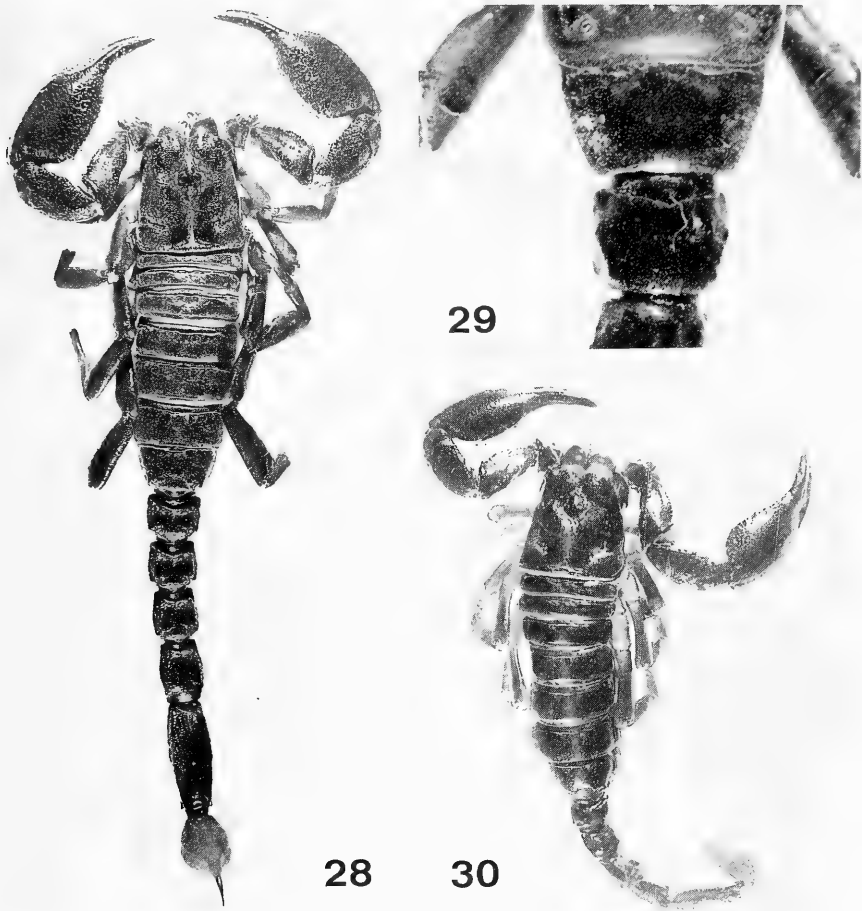
Famille des IURIDAE Thorell, 1876.

Genre **Hadruioides** Pocock, 1893.

Suite aux décisions de KRAEPELIN (1894, 1899) et jusqu'au travail de MELLO-LEITÃO (1945), le genre *Hadruioides* a été considéré comme monotypique, avec une seule espèce *Hadruioides lunatus* (Koch, 1867). Cette situation a sans doute persisté en raison d'une probable méconnaissance du travail de Pocock (1900), où l'auteur revalide diverses espèces anciennes et en crée de nouvelles.

MAURY (1974) publie une révision globale du genre *Hadruioides* et clarifie le statut de cinq espèces et une sous-espèce. Dans son travail il cite 2 espèces et une sous-espèce pour l'Equateur: *Hadruioides maculatus maculatus* (Thorell, 1876), des régions cotières, *Hadruioides maculatus galapagoensis* Maury, 1974, des Galapagos, et *Hadruioides leopardus* Pocock, 1900, signalée pour le sud du Plateau Central. Au cours de la présente étude, nous avons pu examiner du matériel appartenant à *Hadruioides maculatus maculatus* et *Hadruioides maculatus galapagoensis*.

Ainsi que le signale MAURY (1974), *H. maculatus maculatus* habite de toute évidence exclusivement la région côtière du pays. Pour ce qui est du matériel des Galapagos, la condition de sous-espèce de *H. maculatus* nous semble inadéquat. En réalité, ces deux formes bien que vicariantes, ne possèdent pas d'échanges géniques



FIGS 28-30

Teuthraustes festae (holotype-mâle). 28. Vue dorsale. 29. Détail du Vème sternite et du 1er anneau du metasoma, vue ventrale. 30. *Teuthraustes dubius*, femelle de la Vallée du Rio Santiago.

évidents, les Galapagos étant très éloignées de la côte équatorienne. De ce fait, il nous semble que la forme des Galapagos doit être élevée au rang d'espèce, i.e. *H. galapagoensis* Maury.

En ce qui concerne *H. leopardus*, la troisième espèce signalée par MAURY (1974) pour l'Equateur, aucun matériel correspondant aux descriptions données n'a pu être examiné. Deux exemplaires provenant du sud du Plateau Central, affichent plusieurs différences morphologiques par rapport à la description de *H. leopardus* donnée par MAURY (1974).

Hadruoides leopardus a été décrite de Puerto de Eten, Lambayeque au Pérou. Dans sa révision MAURY (1974) signale que le matériel étudié de l'Equateur (Muséum d'Hamburg) présentait plusieurs différences par rapport au matériel type ("En el material estudiado, los 3 lotes procedentes del Ecuador (ZMH) tienen algunas ligeras diferencias con los ejemplares tipos, que tal vez justificarían una separación cuando se cuente con más material de estudio"). Il nous semble que les deux exemplaires de l'Equateur déposés au Muséum de Genève, doivent correspondre à ce matériel "différent" signalé par MAURY (1974). Compte tenu des différences morphologiques observées, nous décidons de trancher sur la question et une nouvelle espèce est proposée pour l'Equateur.

***Hadruoides udvardyi* n. sp.**

H o l o t y p e (♂): Equateur: Province Azuay, Rte Cuenca-Loja, Km 90, 23/7/1990 (A. de Chambrier) (1950 m alt.) (MHNG).

A l l o t y p e (♀): Equateur: Province Azuay, Cuenca Km 102, 9/4/1985 (P. Moret) (1850 m alt.) (MHNG).

E t y m o l o g i e: Le nom spécifique est attribué en hommage au Professeur M.D.F. Udvardy de la "University of California", Sacramento, USA.

D i a g n o s e: Espèce proche d'*Hadruoides leopardus* par la présence de deux carènes sur le Vème sternite (Fig. 9), mais pouvant être différenciée par la vésicule, qui est totalement lisse (chez le mâle et la femelle), comme chez *H. carinatus* (Figs 13 et 14). De cette dernière espèce, *H. udvardyi* se distingue par ses 2 carènes sur le Vème sternite (Fig. 9), tandis que *H. carinatus* en possède quatre (Fig. 10). En outre, les lobes et échancrures des doigts des pinces des pédipalpes présents chez *H. carinatus*, sont absents chez la nouvelle espèce; chez cette dernière les doigts, serrés, ne présentent aucun espace entre eux.

D e s c r i p t i o n fondée sur l'holotype ♂.

Coloration générale jaunâtre avec des nombreuses taches brunâtres sur le corps, pattes et pédipalpes. Quatre bandes longitudinales brunâtres sur les tergites. Anneaux V du Metasoma et telson rougeâtres. Tubercule oculaire et yeux latéraux noirâtres.

M o r p h o l o g i e

Prosoma: Front de la plaque prosomienne légèrement convexe. Sillon longitudinal antérieur faiblement approfondie, arrivant jusqu'au début du tubercule oculaire. Sillon longitudinal postérieur assez discret. Zone semicirculaire antérieure avec une granulation très fine; la surface restante de la plaque prosomienne fortement granulée (Fig. 11). Tergites I à VI avec une granulation moyenne, un peu plus importante sur les bords postérieurs. Tergite VII fortement granulé avec des carènes bien marquées. Sternites I à IV sans granulations, chagrinés. Sternite V avec deux carènes latérales externes bien marquées; des ébouches de carènes latérales internes et une granulation moyenne. Peignes avec 18-17 dents (Fig. 12).

Metasoma: Anneaux I et II avec 8 carènes; les ventrales absentes; anneau V à 5 carènes. Carène intermédiaire ébouchée sur l'anneau III. Telson à vésicule lisse; aiguillon moyennement long et quasi-droit sur les 2/3 antérieurs (Figs 13 et 14).

Pédipalpes: Fémur avec 3 carènes; Tibia à deux carènes; intérieures dorsale et ventrale. Pince sans carènes, lisse. Doigts serrés avec une forme linéaire; tranchant des doigts mobiles avec 7-7 séries de granules; granules accessoires uniquement sur la partie interne. Chélicères avec la dentition caractéristique de la famille. Trichobothriotaxie du type C. néobothriotaxique.

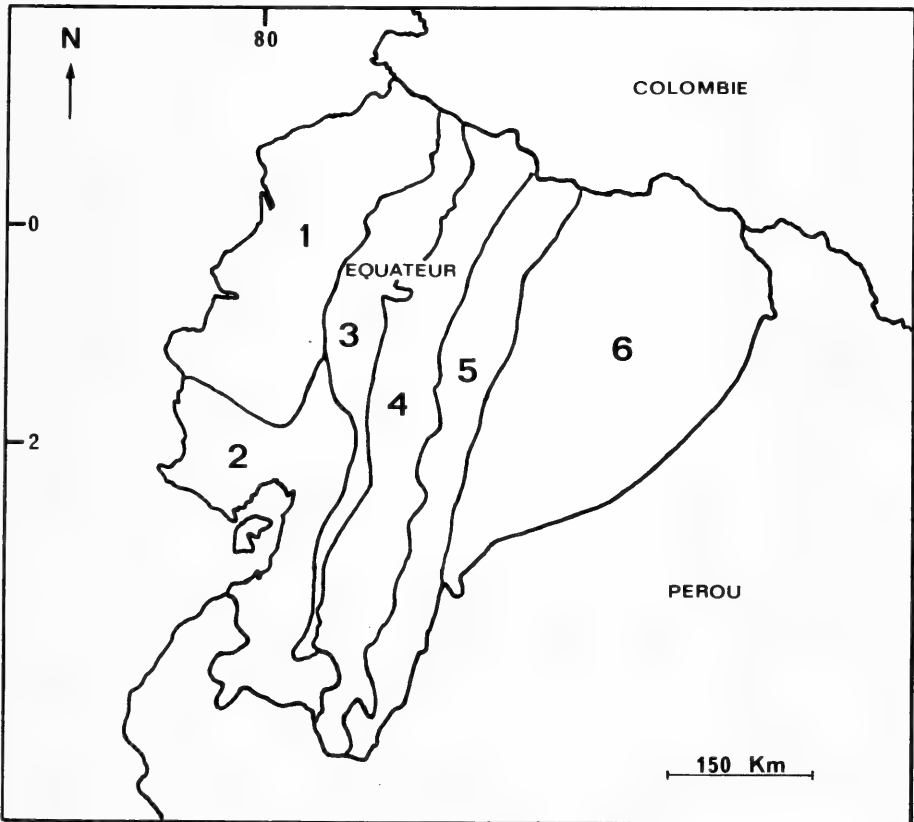


FIG. 31

Zones biogéographiques équatoriennes adoptées dans le travail: 1. Forêt dense de l'Occidente. 2. Régions sèches de l'Occidente. 3. Région andine occidentale. 4. Plateau central. 5. Région andine orientale. 6. Région amazonienne.

Allotype (♀): Coloration semblable à celle du mâle. Segments en général plus trapus, moins allongés (cf. tableau I pour les valeurs morphométriques). Peignes plus petits avec 14-15 dents. Tranchant des doigts mobiles avec 7-7 séries de granules.

TABLEAU I

Mensurations (en mm) des exemplaires décrits.

Ch. mah. / *Chactas mahnerti* n. sp. *Ch. van.* / *Chactas vanbenedeni*.

Ha. udv. / *Hadruioides udvardyi* n. sp.

	<i>Ch. mah.</i>	<i>Ch. van.</i>	<i>Ha. udv.</i> ♂	♀
Prosoma longueur	7,6	6,5	4,4	5,5
Prosoma largeur antérieure	4,9	4,1	2,6	3,4
Anneau caudal I,				
longueur	3,3	3,0	2,2	2,7
largeur	3,7	3,8	3,0	3,6
Anneau caudal V,				
longueur	7,2	6,5	6,0	6,4
largeur	3,1	2,7	2,2	2,7
hauteur	2,9	2,4	2,2	2,4
Vésicule,				
largeur	3,0	2,8	1,9	2,3
hauteur	2,8	2,5	1,5	2,0
Pince,				
largeur	3,3	2,7	1,2	1,9
hauteur	3,2	2,7	1,2	1,8
Doigt mobile,				
longueur	6,1	6,0	4,2	5,0

MATÉRIEL ÉTUDIÉ (Collections déposées à la Pontificia Universidad catolica del Ecuador, Quito, et au Muséum d'histoire naturelle de Genève).

Famille des BUTHIDAE.

- *Tityus asthenes*: Esmeraldas; Cachabi (4 km Rio Arribal; 1 mâle, VIII/88 (O. Delgado). 1 mâle, VII/88 (O. Delgado). Quinde; 1 mâle, XI/88 (G. Onore).
- *Tityus bastosi*: Napo; San Pablo Kantesiya; 1 femelle, 17/IX/86 (J.M. Touzet). 1 femelle, Sc-1595.
- *Tityus forcipula*: Cotopaxi; Las Pampas; 1 immature, I/89 (G. Onore). 1 mâle, X/88 (G. Onore). 1 femelle; 1 immature, X/86 (G. Onore). 1 mâle, I/86 (G. Onore).
- *Tityus pugilator*: Imbabura; Ibarra; 1 femelle, 15/I/89 (O. Bastidas). 1 mâle, 18/IX/88 (V. Aldas). 1 femelle, 15/XII/88 (O. Bastidas). 1 mâle, 20/IX/88 (O. Bastidas). Pichincha; Guayabamba; 1 mâle, 21/I/89 (R. Sandoya). 1 femelle, 27/XII/88 (F. Haro).
- *Tityus simonsi*: Imbabura; Chachimbiro; 2 mâles, 17/XII/84 (S. Abedrabbo). Tungurahua; El Triunfo; 2 femelles, II/89 (G. Onore).

Famille des IURIDAE.

- *Hadruioides galapagoensis*: Galapagos; Isabela; Cerro Azul (1600 m); 10 femelles; 4 immatures, II/86 (G. Onore).

- *Hadruioides maculatus*: Guayas; Playas; 2 femelles, IX/86 (J. Verdin). Salinas Dunas; 1 femelle, 6/IV/85 (P. Moret).

Famille des CHACTIDAE.

- *Teuthraustes atramentarius*:

Cotopaxi; Acaques; 1 mâle, 18/XII/88 (Delgado). Latacunga; 1 immature, X/84 (G. Onore). Imbabura; Atuntaqui; 1 femelle, 15/XI/88 (F. Aloas). Cayambe; 6 mâles; 5 femelles; 3 immatures, VIII/86 (G. Onore). 1 mâle, 8/X/86 (J.M. Touzet). Chachimbiro; 2 mâles; 3 femelles; 2 immatures, 19/XI/84 (L. Coloma). 3 femelles; 1 immature, 17/XI/84 (A. Moya). 1 mâle; 2 femelles; 1 immature (2500 m), XI/84 (A. Salazar). 1 immature, 18/XI/84 (J. Ulofson). 1 mâle; 1 femelle, 18/XI/84 (S. Abedrabbo). 1 mâle, 18/XI/84 (J. Regalado). 1 femelle, 18/XI/84 (S. Luisa). 1 mâle, 18/XI/84 (E. Haelo). 1 mâle, 18/XI/84 (M.A. Calderon). Cotocachi; 1 mâle; 2 femelles, VI/86 (G. Onore). 1 immature, 23/XII/88 (F. Haro). Cyococha; 2 mâles, 4 femelles, VI/86 (G. Onore). Ibarra; 2 mâles; 8 femelles, 3 immatures, I/85 (J. Yepez). 2 mâles; 1 femelle, 2/XI/84 (P. Davila). 2 mâles, VII/86 (A. Gilbert). 1 mâle, 4/VIII/85 (P. Moret). Laguna Cuicocha; 1 mâle; 2 femelles; 3 immatures (3090 m), 11/VIII/90 (A. de Chambrier). Natabuela; 1 femelle, 11/XII/88 (F. Aldas). Napo; Baeza; 1 mâle (1800 m), XI/85 (Briones). El Reventador; 1 femelle; 1 immature, I/85 (G. Onore). Pichincha; Cayambe; 1 mâle, 20/I/85 (T. Arregu). Chillo Gallo; 1 mâle, 2/XI/88 (E. Trujillo). 1 immature, 25/XI/88 (E. Trujillo). El Quinche; 3 immatures, I/86 (F. Correu). Faldas; 3 mâles; 1 femelle; 1 immature, 30/XII/88 (I. Alcoler). Guayllabamba; 1 femelle, 22/I/89 (R. Sandoya). Palmeras; 1 immature, 14/I/89 (T. Leon). 1 mâle, 13/XI/88 (V. Munez). 2 immatures, 25/XII/84 (V. Zav). Pasochoa; 1 mâle, IX/86 (L. Coloma). 1 femelle, 11/XII/88 (Urgiles). 1 femelle, 15/XII/84 (T. Rivera). Pasodor; 1 immature, 15/XII/85 (F. Alban). Puerto Limon; 1 femelle, 16/XII/88 (V. Cachago). 1 mâle, 29/XII/88 (V. Cachago). 1 femelle, 26/XII/88 (V. Cachago). Pululahua; 1 immature, II/85 (M. Vasquez). 1 immature (2600 m), 9/XI/84 (L. Coloma). 1 mâle, XII/84 (P. Ponce). Quito; 4 mâles; 2 femelles, 6/V/85 (S. Stwve). 1 mâle, 21/I/84 (E. Fiallo). 3 mâles, III/85 (F. Rodriguez). 1 mâle, III/85 (C. Ulloa). 1 immature, 26/I/85 (F. Alban). 1 femelle, 2/II/84 (Valencia). 2 immatures, 4/XI/84 (F. Jarrin). 1 mâle (2800 m), 21/X/84 (X. Buitron). 1 mâle; 1 femelle (F. Martinez). 1 mâle; 1 femelle; 1 immature, IV/85 (G. Onore). 1 femelle, 18/XII/84 (S. Abedrabbo). 1 mâle, XII/84 (J. Yepez). 1 femelles, 23/XI/84 (H. Hidalgo). 1 mâle, 10/VI/84 (Valencia). 1 immature, 29/XI/84 (M. Lopez). 1 mâle (2800 m), 25/XI/84 (D. Ortiz). 1 mâle (2800 m°, XII/84 (X. Parmino). 1 mâle, 3/II/85 (M. Bajarano). 1 femelle, 9/XI/85 (L. Roe). 1 mâle, 20/IV/86 (J. Woolfson). 1 femelle, 13/I/86 (P. Vega). 1 femelle, XI/84 (M. Vasquez). 1 femelle, 23/I/85 (C. Rebin). 1 femelle, 19/I/85 (M. Aiguello). 1 femelle, X/89 (U. Mera). 1 mâle, 2/X/84 (Valencia). 1 mâle, I/85 (J. Yepez). 1 femelle; 2 immatures, 14/XI/84 (L. Duque). 1 mâle, 12/I/85 (Valencia). 1 mâle, 2/XII/84 (S. Abedrabbo). 1 immature, 14/XI/84 (X. Buitron). 1 immature, 19/I/85 (E. Martinez). 1 immature, 10/I/86 (S.M. Paz). 2 femelles, 2/XII/85 (S.M. Paz). 1 femelle (2850 m), 2/I/86 (C. Quinton). 1 femelle, 19/I/86 (J. Calern). 1 mâle, IX/84 (A. Sacazar). 1 mâle, 28/I/85 (W. Canon). 1 mâle, X/85 (Briones). 1 femelle, 8/I/89 (C. Ayala). 1 femelle, 5/I/89 (P. Coral). 1 femelle, 5/I/89 (R. Puebla). 1 mâle, 22/XII/88 (D. Delgado). 1 femelle, 7/I/89 (D. Delgado). 1 mâle (3300 m), 30/XII/88 (C. Ayala). 1 femelle, I/88 (Munez). 2 femelles, 31/IX/88 (Haemis). 1 mâle; 1 femelle (3000 m), 22/I/89 (C. Ayala). 1 immature, 8/I/85 (C. Ayala). 1 immature, 5/I/89 (R. Puebla). San Rafael; 1 mâle, 1/I/86 (F. Alban). 1 immature, 24/I/89 (R. Puebla). Santo Domingo; 1 mâle (800 m), 18/XI/84 (L. Torres). 1 mâle, 26/XII/89 (V. Cachago). 1 mâle, 12/X/88 (V. Cachago). Satan Alto; 1 mâle (3000 m), 30/I/85 (I. Rodriguez). Tumbaco; 1 femelle (2400 m), XII/84 (X. Parmino). 1 femelle, I/89 (Figueroa). 1 immature, I/84 (Figueroa).

- *Teuthraustes oculatus*.

Chimborazo; Riobamba-Alansi; 1 femelle (3150 m) (P. Moret). Cotopaxi; Alaquez; 1 femelle, 17/I/88 (F. Haro). Latacunga; 5 mâles; 5 femelles; 1 immature, XI/89 (G. Onore). 1 mâle; 5 femelles; 2 immatures, XI/84 (G. Onore). 1 mâle, X/82 (G. Onore). 5 femelles, XII/88 (Delgado). 1 femelle, XII/88 (P. Coral). 1 femelle, XII/88 (R. Puebla). 1 mâle, 18/XII/84. 1 femelle, 18/XII/88 (F. Haro). 1 immature, 17/I/89 (O. Bastidas). Tungurahua; Ambaro la Peninsula; 1 femelle, 15/XI/85 (X. Taumesto). 1 femelle, 6/IX/85 (Zurietta). 1 immature (?). 2 femelles (?).

- *Teuthraustes whymperei*.

Cotopaxi; Las Pampas; 3 femelles; 2 immatures, XII/84 (G. Onore). 5 mâles; 4 femelles; 4 immatures, V/85 (G. Onore). 5 femelles, III/86 (G. Onore). 1 mâle; 2 femelles; 2 immatures, X/88 (G. Onore). 3 mâles; 6 femelles; 1 immature, IV/85 (G. Onore). 5 femelles, I/86 (G. Onore). 4 femelles, X/86 (G. Onore). 2 mâles; 3 femelles, V/88 (G. Onore). 1 femelle, IV/86 (G. Onore). 2 femelles, V/86 (G. Onore). 1 mâle; 2 femelles; 1 immature, X/85 (G. Onore). 1 femelle, VI/86. 1 mâle; 1 femelle; 1 immature, XII/84 (G. Onore). 1 mâle; 1 femelle; 1 immature (?). Pichincha; Quito; 1 femelle, 19/I/86 (J. Calero). Santo Domingo; 2 femelles, 2 immatures, X/84 (G. Onore). Tungurahua; Banos; 1 immature, 7/X/84 (S. Luisa).

- *Teuthraustes witti*.

Loja; Loja; 3 mâles; 3 femelles; 3 immatures, 24/X/86 (J.M. Touzet). Vilcabamba; 3 femelles (1750 m), 27/VII/90 (A. de Chambrier). Zaruma; 1 mâle (1900 m), 12/IV/85 (P. Morel).

MATÉRIEL TYPE ÉTUDIÉ.

Teuthraustes atramentarius: 1 femelle-type, MNHN (N° 3019-E. Simon), Ecuador, Quito (DeLille). *Teuthraustes dubius*: 1 femelle-type, MIZSUT (Sc-141, ex. 272), Ecuador, Valle di Santiago (L. Festa), 1895-98. *Teuthraustes festae*: 1 femelle-type, MIZUST (Sc-), Ecuador, Valle di Santiago (L. Festa), 1895-98. *Teuthraustes lojanus*: 1 femelle-syntype, NHM (1900-5-10-2-6), Ecuador, Loja, 2000 m (P.O. Simons leg., Purch. Rosenberg). *Teuthraustes oculatus*: 1 mâle-syntype, NHM (1900-5-10-10-12), Ecuador, Sinche-Riobamba, 3000/4000 m (P.O. Simons leg., Purch. Rosenberg). *Teuthraustes ohausi*: 1 femelle-type, ZMH-108, Ecuador, Calamayo, 15/XII/02 (Ohaus). *Teuthraustes rosenbergi*: 1 femelle-syntype, NHM (1898-5-15-1-2), Ecuador, Chimbo (Rosenberg col., Purch.). *Teuthraustes simonsi*: 1 femelle-holotype, NHM (1900-5-10-1), Ecuador, Rio Emboke (P.O. Simons col., Purch. Rosenberg). *Teuthraustes witti*: 2 mâles typus, ZMH, Ecuador, Prov. Loja, Piscobamba, 10/XII/1896 (E. Witt).

MNHN = Muséum National d'Histoire Naturelle, Paris.

NHM = Natural History Museum, Londres.

ZMH = Zoologisches Museum, Hamburg.

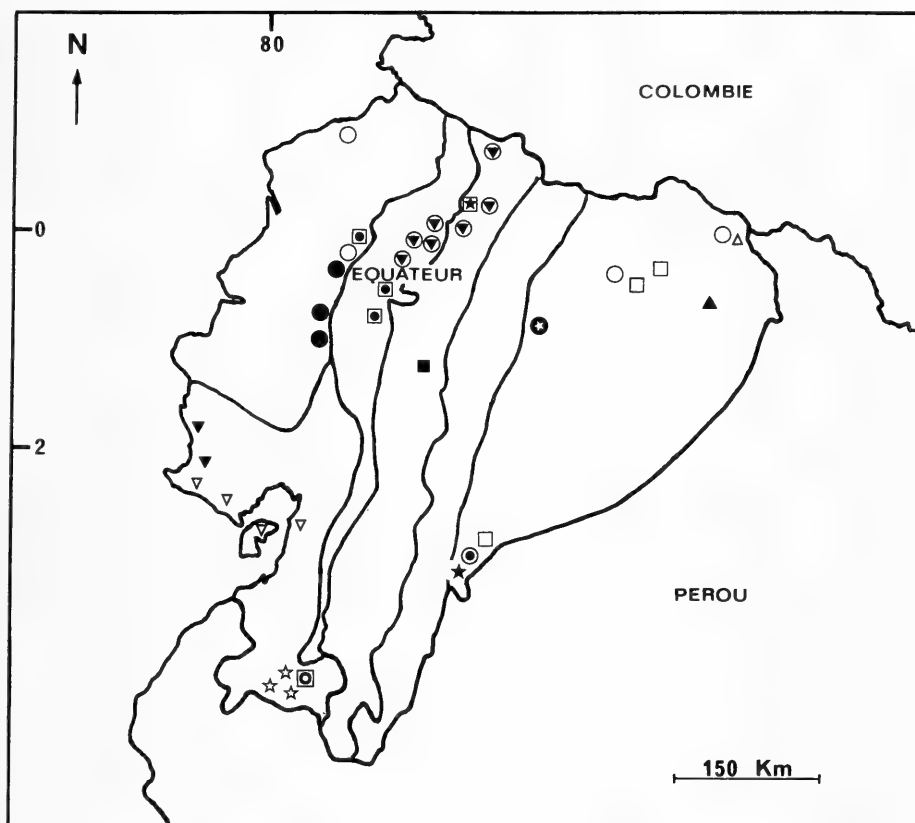
MIZUST = Museo ed Istituto di Zoologia Sistemica, Università di Torino

CONSIDÉRATIONS SUR LA BIOGÉOGRAPHIE ET LA DIVERSITÉ DES ESPÈCES.

BIOGÉOGRAPHIE.

L'Equateur apparaît, au plan biogéographique à la fois comme carrefour mais aussi comme zone de rupture pour les faunes d'origine septentrionale et/ou méridionale (LOURENÇO 1986 A, B). Pour cette raison, différentes tendances faunistiques y sont exprimées (LOURENÇO 1994, B).

Dans le cadre d'un découpage régional plus fin des zones biogéographiques équatoriennes, celui proposé par LEMAIRE (1976) semble bien convenir comme modèle pour la présente étude. Ainsi, cet auteur définit les régions naturelles suivantes pour l'Equateur: 1. Forêt dense de l'Occidente (en continuité du Choco colombien). 2. Régions sèches de l'Occidente. 3. Région andine occidentale (sur le versant ouest du Plateau Central). 4. Plateau Central. 5. Région andine orientale (sur le versant est du Plateau Central). 6. Région amazonienne (Fig. 31).



- | | |
|--------------------------------|------------------------------------|
| ⊙ <i>Ananteris ashmolei</i> | ● <i>Ananteris festae</i> |
| ▼ <i>Centruroides gracilis</i> | ▽ <i>Centruroides margaritatus</i> |
| ○ <i>Tityus asthenes</i> | □ <i>Tityus bastosi</i> |
| ★ <i>Tityus demangei</i> | ☆ <i>Tityus ecuadorensis</i> |
| ▣ <i>Tityus forcipula</i> | △ <i>Tityus garci</i> |
| ⊠ <i>Tityus intermedius</i> | ⊕ <i>Tityus jussanae</i> |
| ♥ <i>Tityus pugilator</i> | ■ <i>Tityus roigi</i> |
| ▲ <i>Tityus silvestris</i> | ⊞ <i>Tityus simonsi</i> |

FIG. 32

Répartition connue des espèces de la famille des Buthidae, en Equateur.

L'analyse de la répartition d'un total de 36 espèces de Scorpions actuellement connues de l'Equateur, appartenant à 8 genres et 4 familles a permis de les classer dans quatre groupes faunistiques: Andin, Guyano-amazonien, Polytopique et Xérophile.

Dans le groupe Andin, le plus diversifié, on trouve les Buthidae: *Ananteris festae*, *T. ecuadorensis*, *T. forcipula*, *T. intermedius*, *T. pugilator*, *T. roigi* et *T. simonsi*.

les Chactidae *Chactas mahnerti*, *Teuthraustes atramentarius*, *T. gervaisi*, *T. lojanus*, *T. oculatus*, *T. ohausi*, *T. simonsi*, *T. whymperei* et *T. witti*, les Iuridae *Hadruiroides leopardus* et *H. udvardyi* (Figs 32 et 33).

Le groupe Guyano-amazonien présente: 1. Des espèces endémiques pour l'Equateur: *Ananteris ashmolei*, *Tityus demangei*, *Tityus jussarae* (Buthidae); *Teuthraustes dubius*, *T. festae*, *Troglotayosicus vachoni* (Chactidae) (Figs 32 et 33). 2. Des espèces à large répartition sur la région amazonienne et/ou sur les forêts humides de la côte pacifique. Ceci étant le cas des Buthidae, *Tityus asthenes*, *T. bastosi*, *T. gasci* et *T. silvestris* (Fig. 32).

Les espèces du groupe xérophile sont peu caractérisées jusqu'à présent, et se confondent, dans certains cas, avec les espèces du groupe polytopique. Ainsi, *Brachistosternus (B) ehrenbergi* et *Hadruiroides maculatus* (Fig. 34) sont des espèces Xérophiles, la première d'origine méridionale et la seconde à répartition plutôt locale.

Les espèces du genre *Centruroides*, *C. gracilis* et *C. margaritatus* (Fig. 32) peuvent être définies en tant que polytopiques, bien que également Xérophiles en Equateur. Finalement *Centruroides exsul* et *Hadruiroides galapagoensis* sont des espèces endémiques de Galapagos. *H. galapagoensis* a des affinités avec *H. maculatus* et trouve ses origines sur la faune continentale (Equateur/Pérou). Pour *C. exsul*, ses origines doivent se retrouver plutôt en Amérique centrale où parmi des espèces affines, on devra définir son vicariant. En Amérique du Sud aucun vicariant potentiel n'est présent (SISSOM & LOURENÇO, 1987).

Si on tient compte de l'ensemble des éléments qui composent les faunes orientale et occidentale, on constate que parmi les espèces étudiées, une seule, *Tityus asthenes* est présente sur les deux versants du Plateau Central (Fig. 32).

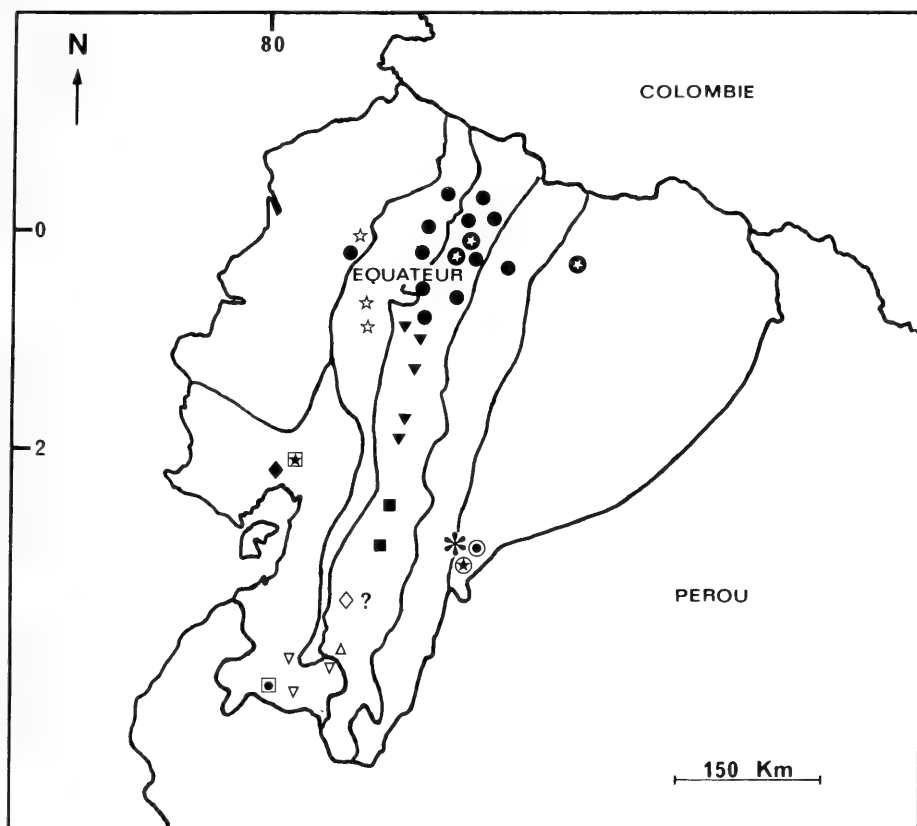
Les Scorpions apparaissent de toute évidence comme un matériel excellent pour l'étude biogéographique d'une faune donnée (LOURENÇO 1994c, sous presse, A). L'Equateur, par sa situation géographique, est un véritable carrefour pour la richesse faunistique de diverses régions très importantes au sein du domaine néotropical. Une telle situation, associée à sa superficie réduite, fait de ce pays un lieu de synthèse idéal pour de telles recherches.

DIVERSITÉ.

Au moment où la biodiversité est au centre du débat dans les études traitant de la biogéographie et d'écologie évolutives (WILSON, 1988), il semble utile de tenter de situer la diversité biologique équatorienne parmi celles de quelques autres régions d'Amérique tropicale.

Il est certain que tout essai d'estimer précisément la biodiversité dans une région comme celle de l'Equateur est nécessairement biaisé car il s'agit là d'une unité politique et non d'une région naturelle. Malgré ce type de handicap, quelques données comparatives peuvent être affichées à titre d'exemple, dans le tableau suivant.

La richesse spécifique présente en Equateur, déjà remarquable en valeur absolue, se montre très importante quand on la compare à celles d'autres pays ou régions étudiées, surtout en tenant compte de leurs superficies respectives.



- | | |
|-------------------------------------|----------------------------------|
| ◆ <i>Chactas camposi</i> | ⊛ <i>Chactas mahnerti</i> |
| ● <i>Teuthraustes atramentarius</i> | ⊙ <i>Teuthraustes dubius</i> |
| ⊛ <i>Teuthraustes festae</i> | ■ <i>Teuthraustes gervaisi</i> |
| △ <i>Teuthraustes lojanus</i> | ▼ <i>Teuthraustes oculatus</i> |
| ▣ <i>Teuthraustes ohausi</i> | ⊞ <i>Teuthraustes rosenbengi</i> |
| ◇ <i>Teuthraustes simonsi</i> | ☆ <i>Teuthraustes whymperi</i> |
| ▽ <i>Teuthraustes witti</i> | * <i>Troglotayosicus vachoni</i> |

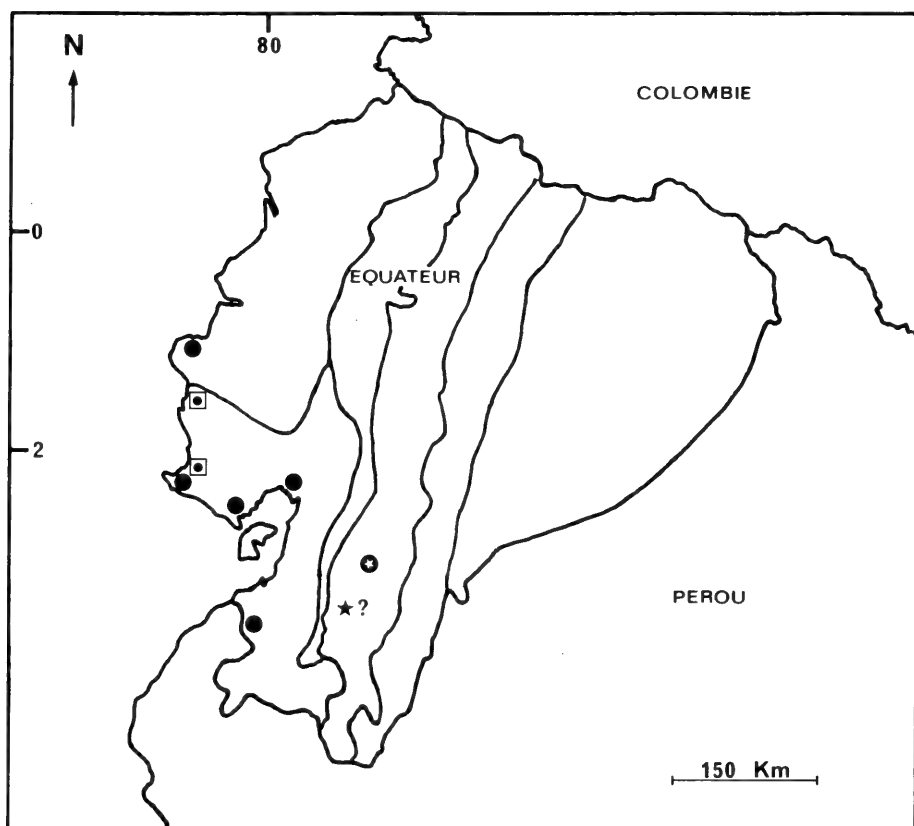
FIG. 33

Répartition connue des espèces de la famille des Chactidae, en Equateur.

Les chiffres appellent évidemment des réserves étant donné l'inégalité de la connaissance des faunes de ces pays ou régions, pour la plupart encore très sous-estimées.

Pour l'Equateur, le nombre d'espèces recensées jusqu'à présent peut être considéré comme proche de la réalité, d'autant plus que sur un total des 36 espèces, 24 sont

Région/pays	Superficie en km ²	Nb. Fam.	Nb. Gen.	Nb. Esp.	% espèces endémiques
Paraguay	406752	2	6	12	18,2
Equateur	270670	4	8	36	66,7
Guyane Fr.	91000	3	6	18	22,3
Panama	75650	4	6	12	16,7
Costa Rica	50700	4	7	13	38,5



□ *Brachistosternus (B.) ehrenbengi*

● *Hadrnoides maculatus*

★ *Hadrnoides leopardus*

★● *Hadrnoides udvandyi*

FIG. 34

Répartition connue des espèces de la famille des Buthriuridae et des Iuridae, en Equateur.

endémiques de ce pays, soit 66,7%. Néanmoins, plusieurs Provinces demeurent peu prospectées (e.g. Pastaza et Morona-Santiago en Amazonie). De nouvelles collectes devront encore révéler de nombreuses espèces nouvelles.

Globalement, l'Equateur appartient à une région qui possède une des plus importantes diversités au monde, en ce qui concerne sa faune des Scorpions. Cette région comprend aussi le sud de la Colombie, le nord du Pérou et l'ouest du Brésil (LOURENÇO, 1994c). C'est sur l'ensemble de cette région que devront se poursuivre les efforts d'inventaire pour une meilleure évaluation et la mise en valeur de cette très grande biodiversité.

En plus des apports fondamentaux qu'autorisent les études conjointes de la biogéographie évolutive et de la diversité biologique, ces études contribuent directement à la mise en place des programmes de conservation. A présent les études sur la biogéographie évolutive et la biodiversité, avec une approche tournée vers la conservation, comptent parmi les plus nombreuses (LOURENÇO & BLANC, 1994). Or ceci correspond à l'aspect appliqué de la biogéographie, ou "applied biogeography" qui est égale à la conservation, dans le sens défini par PIANKA (1988).

Dans le cadre précis de l'Equateur, des études sont actuellement en développement dans le but de bien délimiter une zone prioritaire à la création d'un Parc binational entre l'Equateur et le Pérou (cf. projet de la Fundacion Natura-Ecuador et Fundacion Proterra-Pérou). Les résultats apportés par la présente publication, même s'ils peuvent être considérés comme le "quick and dirty" processus d'inventaire et de "monitoring" définis par EHRLICH (1992), contribuent de manière certaine à l'ensemble des données requises pour une bonne délimitation de ces futures unités de conservation.

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Nématodes de Poissons du Paraguay. VIII. Habronematoidea, Dracunculoidea et Ascaridoidea

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Nematode parasites of Paraguayan Fishes. VIII. Habronematoidea, Dracunculoidea and Ascaridoidea. - Six species are recorded from fresh-water fishes of Paraguay: *Spinitectus aff. pachyuri*, parasite of *Auchenipterus nuchalis*, is characterized by 6 pairs of preanal papillae on the male tail. *Philometra paraguayensis* sp. nov., parasite of *Salminus maxillosus*, known only by one male specimen, differs from other Philometrid males in having a wider body and one pair of double preanal papillae. *Sprentascaris hypostomi* is recorded from *Cochliodon cochliodon*; the specimens differ from the type specimens in having lips with more developed horn-like protrusions. Juvenile females or fourth-stage larvae of *Goezia* sp. (from *Salminus maxillosus*), *Hysterothylacium* sp. and *Raphidasascaroides* sp. (from *Platydoras costatus*) are described.

Key-words: Spinitectus - Philometra - Ascaridoidea - Nematoda - Fish - Paraguay.

Poursuivant notre étude des Nématodes parasites de Poissons du Paraguay récoltés par les expéditions zoologiques du Muséum d'Histoire Naturelle de Genève (PETTER 1984, 1989, 1990, 1994, PETTER & CASSONE 1984, PETTER & DLOUHY 1985, PETTER & MORAND 1988), nous décrivons ici une espèce du genre *Spinitectus* (Habronematoidea) très voisine de *S. pachyuri* Petter, 1984, une espèce nouvelle de *Philometra* (Dracunculoidea) et signalons des spécimens appartenant à trois genres d'Ascaridoidea (*Goezia* sp., *Hysterothylacium* sp. et *Raphidasascaroides* sp.), dont la diagnose spécifique n'a pu être faite en l'absence de mâles et de femelles mûres, mais dont la présence au Paraguay est à mentionner; des adultes des genres *Hysterothylacium* et *Raphidasascaroides* sont signalés pour la première fois dans les eaux douces sud-américaines. De plus, *Sprentascaris hypostomi* a été identifié chez un nouvel hôte.

MATÉRIEL ET MÉTHODE

Les viscères des Poissons sont fixés au formol à 4% au moment de l'autopsie, puis triés au laboratoire à Genève; les nématodes recueillis sont conservés dans l'alcool à 70% et éclaircis au lactophénol pour l'étude. Le matériel étudié est déposé au Laboratoire de Biologie Parasitaire du Muséum national d'histoire naturelle de Paris (MNHN) et au Muséum d'histoire naturelle de Genève (MHNG).

Toutes les mensurations sont exprimées en μm .

HABRONEMATOIDEA, CYSTIDICOLIDAE

Spinitectus aff. pachyuri Petter, 1984

(fig. 1)

Matériel étudié: un mâle et 2 extrémités antérieures n° MNHN 278 BC. Hôte: *Auchenipterus nuchalis* (Spix) (Auchenipteridae, Siluriformes) (n° de terrain Py 4291), Rio Ipane à Belen, Prov. Concepcion, 12.10.1985. Une extrémité postérieure mâle, 1 extrémité antérieure et 1 larve femelle n° MNHN 250 BC; 1 extrémité postérieure mâle et 2 extrémités antérieures n° MHNG 985.1002 (n° de terrain Py 4224). Hôte: *Auchenipterus nigripinnis* (Boul.), Rio Jeju-Guazu, Prov. San Pedro, 9.10.1985.

DESCRIPTION: corps long et grêle; anneaux épineux interrompus le long des axes médians et des axes latéraux. Premiers anneaux situés antérieurement à l'extrémité du pharynx; espacement des anneaux dans la région antérieure variant de 20 à 30 μm pour les 3 premiers anneaux et de 25 à 40 μm pour les anneaux suivants; l'espacement augmente vers la région postérieure et les demi-anneaux ventraux et dorsaux sont situés à des niveaux transversaux différents; chez le mâle holotype, au delà du milieu du corps, les anneaux deviennent invisibles au microscope optique, on observe seulement quelques très petites épines éparses. Nombre d'épines par anneau: 16 à 18. Epines fines et pointues, longues de 15 à 30 μm dans la région antérieure, et diminuant progressivement de taille dans les anneaux suivants (10 μm après le 16ème anneau, 5 μm au milieu du corps chez le mâle holotype). Ouverture buccale ovale, pseudo-lèvres latérales limitées aux axes latéraux et laissant libres les parties dorsale et ventrale de l'ouverture buccale; les bords antérieurs dorsaux et ventraux du pharynx saillent hors de l'ouverture buccale en 2 crêtes cuticulaires dressées.

Amphides et papilles submédianes non situées sur les pseudo-lèvres; chaque pseudo-lèvre porte deux petites protubérances apicales. Pharynx très long, évasé latéralement à l'extrémité antérieure; oesophage musculaire court; oesophage glandulaire très long. Très petites deirides situées entre le premier et le deuxième anneau d'épines. Pore excréteur situé immédiatement en avant ou immédiatement en arrière du 6ème anneau d'épines.

Mâle: extrémité postérieure enroulée en plusieurs tours de spire. Minces ailes caudales présentes. Six paires de papilles pré-cloacales groupées deux à deux; six paires de papilles post-cloacales (y compris les phasmides). Ornementation pré-cloacale faite de rangées de petites crêtes rectangulaires débutant au niveau des paires cloacales les plus antérieures et s'étendant jusqu'à 1150 μm de l'extrémité postérieure chez le mâle holotype; le nombre maximum de rangées de crêtes est de cinq, les différentes rangées débutant à des niveaux différents. Spicules minces, arrondis à leur extrémité distale; spicule gauche coudé en son milieu; rapport spicule droit/spicule gauche = 1/2.

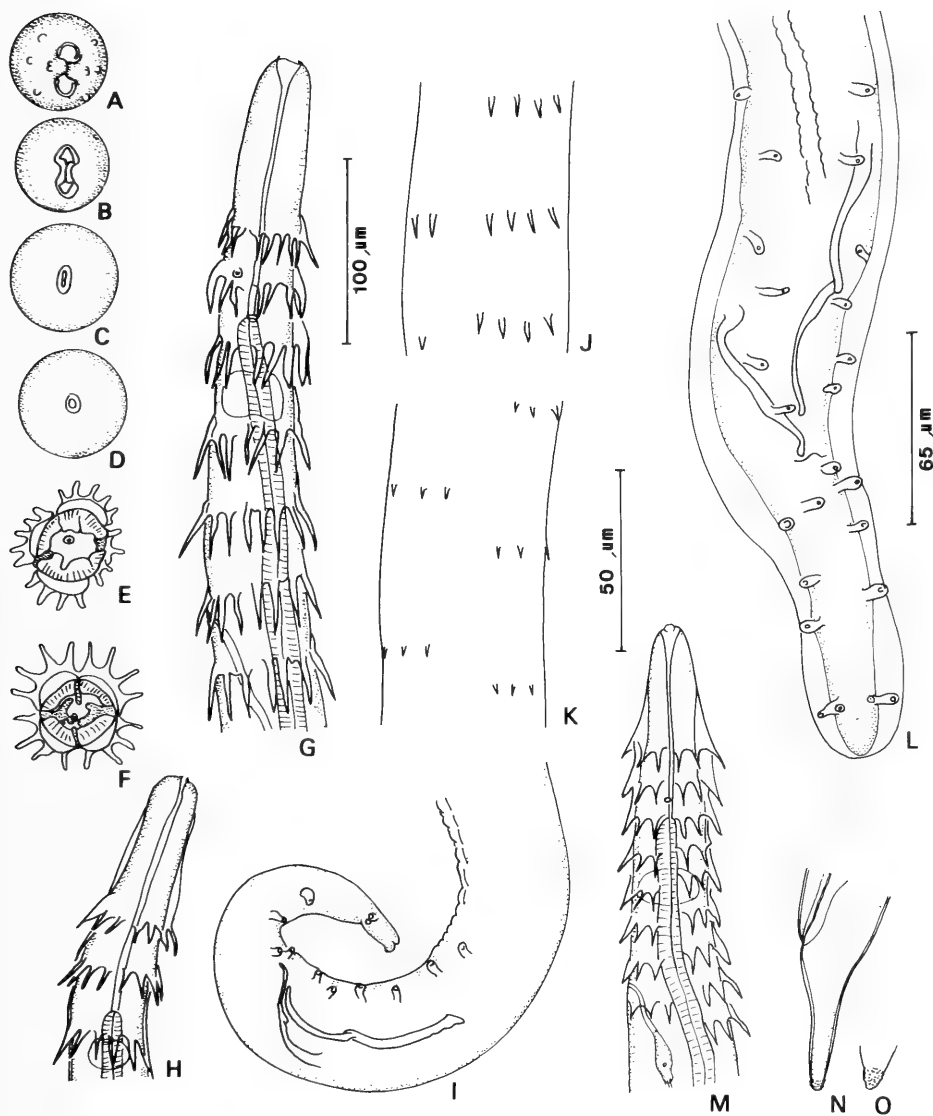


FIG. 1

Spinitectus aff. *pachyuri* Petter, 1984. A, vue apicale; B, C, D, coupes optiques au niveau du pharynx de plus en plus profondes; E, F, coupes transversales au niveau du 1er et du 2ème anneau d'épines; G, région antérieure, vue latérale; H, région antérieure, vue médiane; I, mâle extrémité postérieure, vue latérale; J, K, mâle, portions du corps: J, niveau du 15ème anneau d'épines; K, niveau des derniers anneaux; L, mâle, région postérieure, vue ventrale; M, N, O, larve femelle: M, région antérieure, vue latérale; N, queue, vue latérale; O, extrémité caudale.

Echelles: A, B, C, D, K, O: 50 μ m; E, F, H, I, J, M, N: 100 μ m; L: 65 μ m.

Mensurations du mâle: long. 8400; larg. maximale 70; pharynx 135; oesophage musculaire 215; oesophage glandulaire 1960; distance extrémité antérieure - anneau nerveux 170; - deirides 115; - pore excréteur 280; - premier anneau d'épines 90; spicule gauche 100; spicule droit 50; queue 100.

Mensurations des 4 extrémités antérieures: pharynx 80/110/118/130; distance extrémité antérieure - anneau nerveux 110/145/150/160; - deirides 85/70/105/110; - pore excréteur 200/170/240/235; - premier anneau d'épines 70/55/90/80.

Mensurations des deux extrémités postérieures mâles: spicule gauche 100/100; spicule droit 50/55; queue 120/100.

Larve femelle: longueur 3150; la région antérieure présente le même aspect que celle de l'adulte, mais le pharynx est relativement plus long, les deirides sont situées entre le 2ème et le 3ème anneau d'épines, et le pore excréteur entre le 7ème et le 8ème anneau; ébauche vulvaire située aux 2/3 du corps. Queue conique, à extrémité arrondie couverte de minuscules épines.

DISCUSSION: sept espèces du genre *Spinitectus* sont actuellement connues chez les Poissons d'eau douce sud-américains: parmi celles-ci, quatre s'écartent de nos spécimens par le grand nombre d'épines présentes sur chaque anneau (plus de douze par demi-anneau dans la région oesophagienne d'après les figures): *S. asperus* Travassos, Artigas & Pereira, 1928, décrite uniquement sur des femelles, *S. rodolphiheringi* Vaz & Pereira, 1934, *S. jamundensis* Thatcher & Padilha, 1977, et *S. sternopygi* Petter, 1984; de plus, *S. rodolphiheringi*, *S. jamundensis* et *S. sternopygi* ne présentent que quatre paires de papilles pré-cloacales (ce caractère n'est pas suffisant à lui seul pour différencier les espèces, en effet le nombre de papilles pré-cloacales ne semble pas bien fixé pour *S. jamundensis*: dans la description originale, THATCHER & PADILHA indiquent trois ou quatre paires pré-anales et les spécimens décrits par PETTER & MORAND (1988) présentent quatre papilles pré-cloacales du côté droit et six papilles du côté gauche). Les espèces *S. yorkei* Travassos et al. (1928) et *S. multipapillata* décrite en Equateur par PETTER (1987) ont un plus grand nombre de papilles pré-cloacales (respectivement quinze paires et huit paires); de plus, chez *S. multipapillata*, le pore excréteur est situé entre le 4ème et le 5ème anneau d'épines, alors que chez tous les spécimens adultes décrits ci-dessus, il est au voisinage du 6ème anneau (la valeur spécifique de ce caractère a été soulignée par MORAVEC 1979). *S. pachyuri* Petter, 1984, parasite d'un Sciaenidae (*Pachyurus bonariensis*) et connue uniquement par des femelles, est très voisine de nos spécimens par la structure apicale, la disposition et la taille des épines et l'ensemble des dimensions, et en particulier par la position du pore excréteur situé au voisinage du 6ème anneau d'épines.

DRACUNCULOIDEA, PHILOMETRIDAE

***Philometra paraguayensis* n. sp.**

(fig. 2)

Matériel-type: mâle holotype n° MNHN 401 BC. Hôte: *Salminus maxillosus* Valenciennes (Characidae, Characiformes) (n° de terrain Py 4989), rio Parana en face de Puerto El Dorado, prov. Itapua, 8.2.1987.

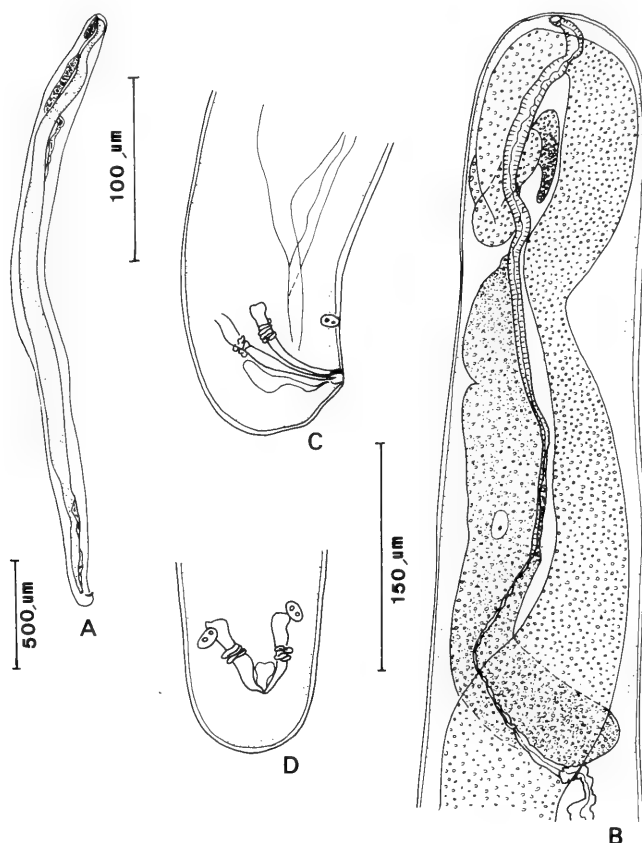


FIG. 2

Philometra paraguayensis n. sp. A, corps entier; B, région antérieure; C, extrémité postérieure, vue latérale; D, extrémité postérieure, vue ventrale.

Echelles: A: 500 µm; B: 150 µm; C,D: 100 µm.

DESCRIPTION: nématode court, cylindrique, légèrement incurvé ventralement à l'extrémité postérieure. Cuticule finement striée transversalement. Extrémité antérieure arrondie. Bouche ronde; papilles céphaliques invisibles. Oesophage très grêle, non élargi à l'extrémité antérieure; glande oesophagienne proéminente, accolée à l'oesophage dans ses 2/3 postérieurs, avec un gros noyau situé en son milieu. Intestin mince, peu visible. Pore excréteur et anneau nerveux invisibles. Testicule épais, s'étendant antérieurement jusqu'à l'extrémité antérieure du corps, où il se recourbe en crosse. Extrémité postérieure arrondie, dépourvue de lobes latéraux. Cloaque subterminal. Une paire de papilles doubles pré-cloacales subventrales, situées très en avant de l'ouverture

cloacale. Spicules courts, égaux, effilés à l'extrémité. Gubernaculum aminci dans sa moitié postérieure.

Mensurations: long. 2760; larg. maximale 200; spicules 70; gubernaculum 45.

DISCUSSION: par sa structure oesophagienne et la forme de l'extrémité postérieure, ce spécimen appartient à la famille des Philometridae, sous-famille des Philometrinae; il ne peut être attribué à un genre précis car la distinction des genres chez les Philometridae est basée sur la morphologie des femelles gravides; six espèces de la sous-famille ont été décrites chez les Poissons d'eau douce sud-américains: deux espèces parasites d'*Arapaima gigas* (Osteoglossiformes), *Nilonema senticosa* Baylis, 1927 et *Rumai rumai* Travassos, 1960; trois espèces parasites de Siluriformes: *Philometra* (P.) *amazonica* Travassos, 1960, *Philometra* (*Alinema*) *alii* Rasheed, 1963 et *Philometra* (P.) *baylisi* Vaz & Pereira, 1934; une espèce parasite de *Salminus hilarii* (Characiforme), *Philometroides maplestoni* (Travassos *et al.*, 1928); les mâles ont été décrits uniquement chez *Philometra* (*Alinema*) *alii* par INGLIS & OGDEN (1964); ils se différencient de notre spécimen par un oesophage dilaté antérieurement, des spicules inégaux et la disposition des papilles cloacales. Il existe très peu de caractères morphologiques permettant d'apparier les mâles et les femelles d'une même espèce chez les Philometridae, et l'appariement est basé principalement sur la présence des deux sexes dans un même individu hôte; aucun caractère distinctif de notre spécimen ne permet de l'attribuer à l'une des cinq espèces connues uniquement par les femelles et qui parasitent des hôtes d'espèces différentes et provenant de localités éloignées. Ce mâle présente par rapport aux autres mâles de Philometridae connus des caractères atypiques: l'épaisseur du corps et la situation très antérieure des papilles cloacales. Nous considérons par conséquent qu'il appartient à une espèce nouvelle que nous proposons d'appeler *Philometra* (?) *paraguayensis* n. sp.; la découverte éventuelle de femelles de cette espèce permettra de préciser son appartenance générique.

ASCARIDOIDEA, ANISAKIDAE

***Sprentascaris hypostomi* Petter et Cassone, 1984**

(fig. 3)

Matériel: un mâle et 1 femelle n° MNHN 248 BC (n° de terrain Py 4305); 1 femelle n° MNHN 252 BC (n° de terrain Py 4382) et 2 femelles n° MHNG 985.1003 (n° de terrain Py 4306). Hôte: *Cochliodon cochliodon* (Kner) (Loricariidae, Siluriformes), Rio Itane à Belén et Estancia laguna Negra, prov. Concepcion, Paraguay, 12.10.1985 et 16.10.1985.

Sprentascaris hypostomi a été décrit par PETTER & CASSONE (1984) chez *Hypostomus* sp. (Loricariidae) au Paraguay; MORAVEC *et al.* (1990) la redécrit au Brésil chez quatre autres espèces de Loricariidae (*Plecostomus albopunctatus*, *P. commersoni*, *P. derbyi* et *Ancistrus cirrhosus*). Les spécimens parasites de *Cochliodon cochliodon* diffèrent de la description originale: 1) par la forme des lèvres: celles-ci présentent deux paires de cornes membraneuses dans lesquelles s'engagent des prolongements latéraux de la pulpe labiale; ces cornes, très développées chez les parasites de *Cochliodon cochliodon* (fig. 3, C,D), sont à peine ébauchées chez les spécimens décrits par PETTER & CASSONE; 2) par des spicules dont l'extrémité distale est

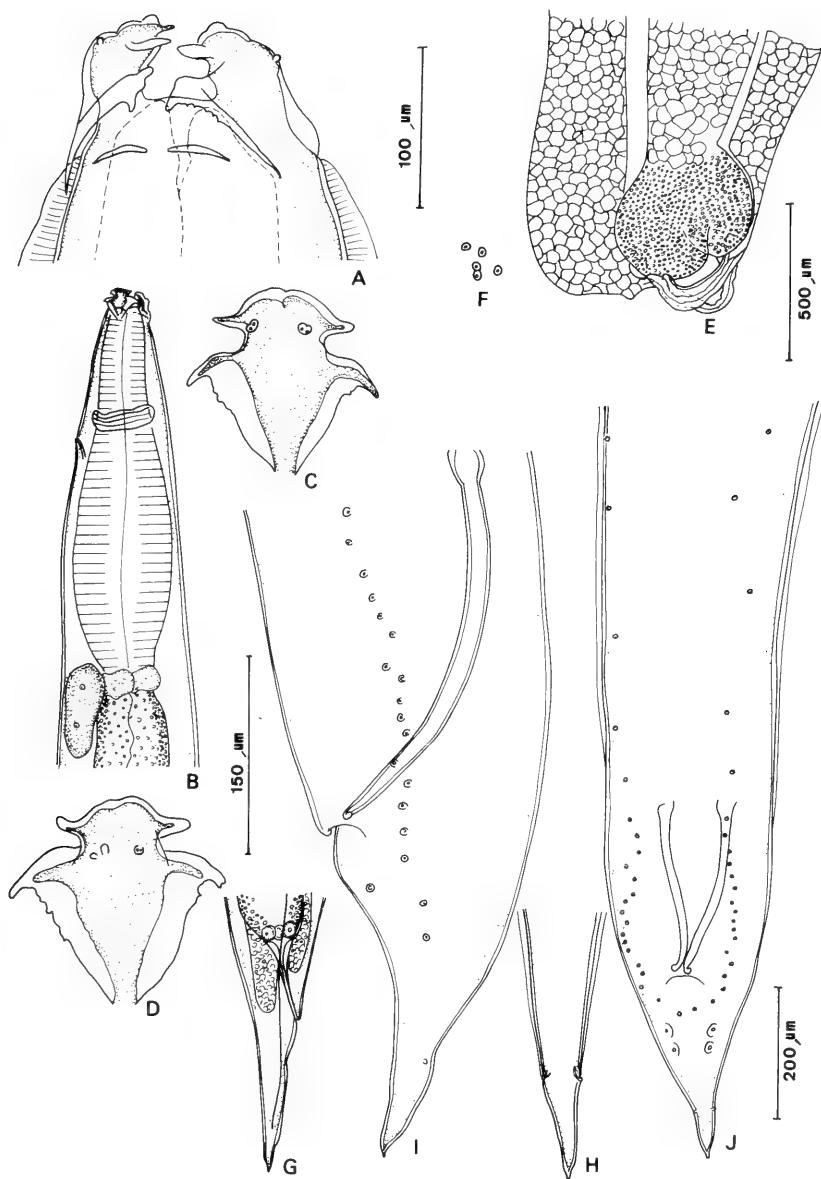


FIG. 3

Sprentascaris hypostomi Petter & Cassone, 1984. A, mâle, extrémité antérieure, vue ventrale; B, mâle, région antérieure, vue latérale; C, femelle, lèvre dorsale; D, femelle, lèvre latéro-ventrale; E, femelle fécondée, réceptacle séminal à la jonction trompe-uterus; F, spermatozoïdes dans le réceptacle séminal; G, femelle, extrémité postérieure, vue latérale; H, femelle, extrémité postérieure, vue médiane; I, mâle, extrémité postérieure, vue latérale; J, mâle, région postérieure, vue ventrale. Echelles: A,C,D,F: 100 µm; B,E,G: 500µm; H,J: 200 µm; I: 150 µm.

retroussée (fig.3, I,J). Chez les spécimens décrits par MORAVEC *et al.*, la forme des lèvres est intermédiaire entre celle de la description originale et celle des parasites de *Cochliodon cochliodon*; nous considérons donc ces différences comme des variations intraspécifiques locales.

MORAVEC *et al.* (1990) réduisent le genre *Sprentascaris* au rang de sous-genre de *Raphidascaris*: les caractères différenciant les deux genres, et en particulier la présence d'une ornementation cuticulaire interlabiale chez *Sprentascaris* ne leur paraissent pas avoir une valeur générique, car une petite élévation cuticulaire triangulaire entre les bases des lèvres sub-ventrales est signalée par SMITH (1984) chez *Raphidascaris acus*.

La même année, BRUCE (1990) limite le genre *Raphidascaris* à l'espèce-type, *R. acus*. D'autre part, sans remettre en question la validité du genre *Sprentascaris*, il rapproche *Sprentascaris hypostomi* de *Raphidascaroides africanus* Khalil & Oyetayo, 1988, les deux espèces présentant selon lui la même morphologie céphalique; à notre avis, les deux espèces ne présentent pas d'affinités particulières en dehors de la forme allongée des lèvres que nous considérons comme un caractère de convergence. Quoiqu'il en soit, il ressort de ces travaux divergents qu'une révision des espèces de la famille des Raphidascaridinae prenant en compte la phylogénie serait nécessaire, ainsi qu'une étude de l'homologie entre les structures interlabiales des différentes espèces. Dans l'état actuel des connaissances, nous préférons conserver le genre *Sprentascaris*, car les trois espèces qui le composent (*S. mahnerti* Petter & Cassone, 1984, *S. pimelodi* Petter & Cassone, 1984 et *S. hypostomi* Petter & Cassone, 1984) présentent outre l'existence de pièces cuticulaires interlabiales, plusieurs caractères communs ayant une valeur évolutive (petite taille, uterus courts, oeufs embryonnés au moment de la ponte), que ne possèdent pas les autres espèces.

Goezia sp.

(fig. 4)

Matériel: une larve du 4ème stade ou femelle juvénile n° MNHN 404 BC (n° de terrain Py 4976). Hôte: *Salminus maxillosus* Valenciennes (Characidae, Characiformes), Rio Parana en face de Candelaria, 13.12.1986. Co-parasites: *Spirocamallanus paraguayensis*; larves d'Ascarides.

DESCRIPTION: nématode court et trapu. Cuticule munie d'anneaux transversaux d'épines qui s'étendent de l'extrémité antérieure jusqu'à la pointe caudale. Nombre d'épines par anneau dans la région antérieure: environ 80; épines très petites (longueur maximale dans la région antérieure: 4 à 5 µm; dans la moitié postérieure du corps: 1 à 2 µm). Lèvres présentant l'aspect habituel au genre *Goezia*. Petit ventricule plus large que long; caecum intestinal court; appendice oesophagien très long; queue courte et conique.

Principales mensurations: long. 2300; larg. maximale 75; oesophage 270; ventricule: long. 20; larg. 25; caecum intestinal 110; appendice oesophagien 960; queue 60.

DISCUSSION: deux espèces du genre *Goezia* ont été décrites chez les Poissons dulçaquicoles sud-américains: *G. spinulosa* (Diesing, 1839) et *G. intermedia* Rasheed, 1965; MORAVEC *et al.* (1990) décrivent également une larve du 4ème stade de *Goezia* sp.

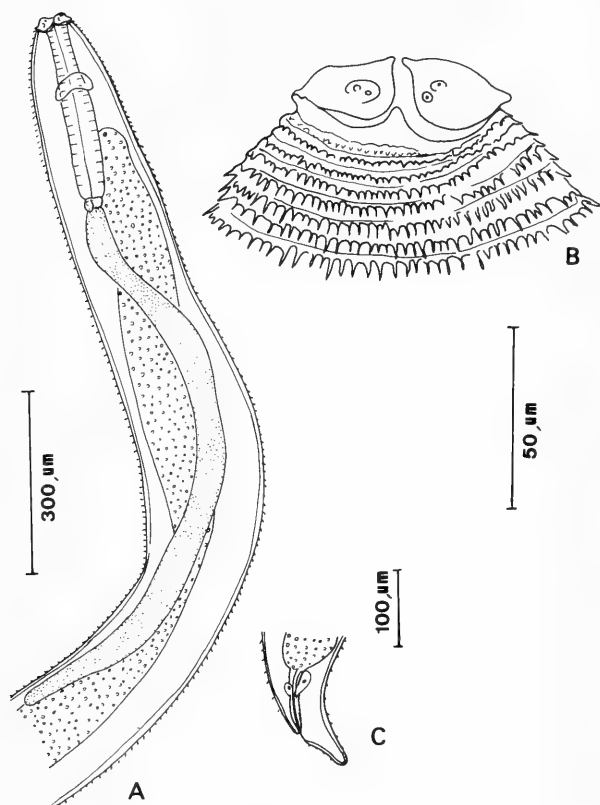


FIG. 4

Goezia sp. A, région antérieure, vue latérale; B, extrémité antérieure, vue latérale; C, extrémité postérieure, vue latérale. Echelles: A: 300 µm; B: 50 µm; C: 100 µm.

récoltée chez des Characidae et Ageneiosidae au Brésil. Par l'absence de petits nodules à l'extrémité de la queue, le spécimen correspondrait plutôt à *G. spinulosa* (voir Rasheed 1965), cependant la diagnose spécifique ne peut être faite sans connaître la disposition des papilles caudales du mâle.

Hysterothylacium sp.

(fig. 5)

Matériel : 1 région antérieure n° MNHN 304 BC (n° de terrain Py 5099) (co-parasite: *Raphidascaroides* sp.) ; 1 larve du 4ème stade n° MNHN 316 BC (n° de terrain Py 5097). Hôte: *Platydoras costatus* (L.) (Doradidae, Siluriformes), Villeta, prov. Central, 14.11.1987.

DESCRIPTION : nématodes à corps cylindrique, amincis à l'extrémité antérieure. Cuticule striée transversalement. Bouche entourée par 3 grandes lèvres pédonculées, légèrement plus larges que hautes, brusquement rétrécies au niveau de leur tiers antérieur; ailes labiales munies de lobes dirigés postérieurement; crêtes denticulées absentes; pulpe labiale avec deux lobes antérieurs arrondis; deux papilles doubles sur la lèvre dorsale, une papille double, une papille simple et une amphide sur chaque lèvre latéroventrale;

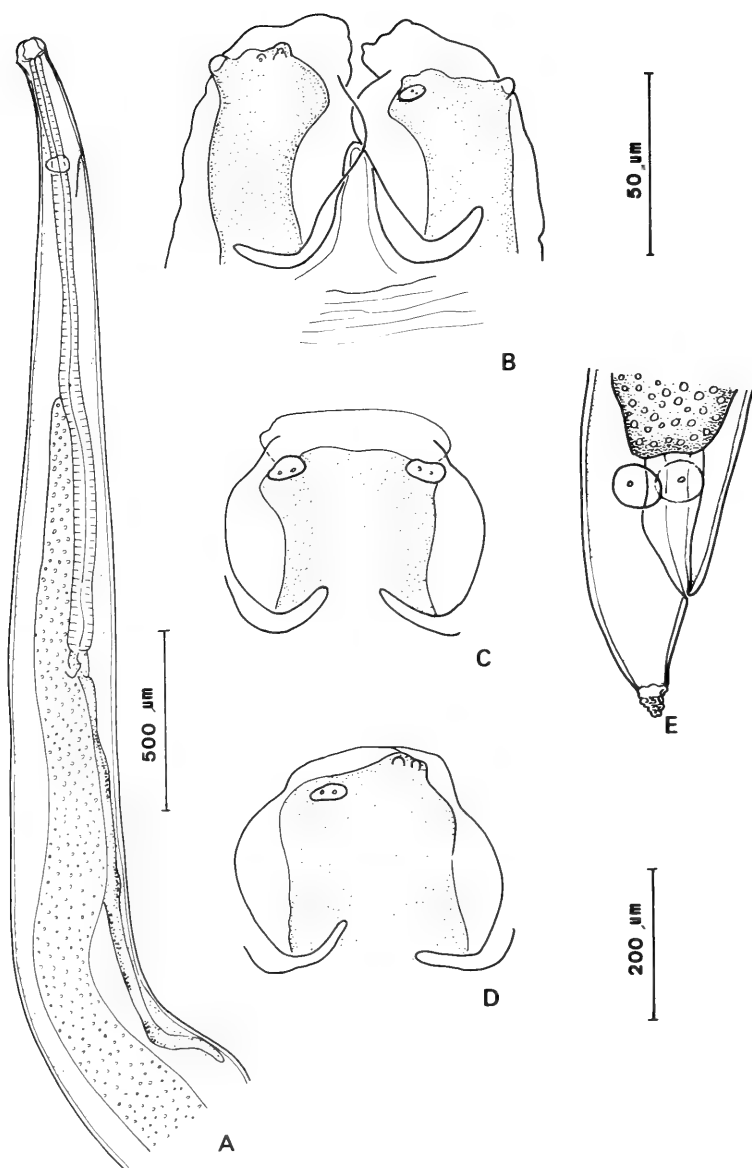


FIG. 5

Hysterothylacium sp. A, région antérieure, vue latérale; B, extrémité antérieure, vue latérale; C, lèvres dorsale; D, lèvres latéro-ventrale; E, extrémité caudale, vue latérale. Echelles: A: 500 µm; B,C,D: 50 µm; E: 200 µm.

interlabia bien développés, coniques, mesurant la moitié de la longueur des lèvres. Ailes latérales absentes. Pore excréteur au niveau de l'anneau nerveux. Oesophage long, cylindrique. Petit ventricule plus large que long. Appendice oesophagien long et grêle. Caecum intestinal épais, mesurant un peu moins de la moitié de la longueur de l'oesophage. Queue conique, à extrémité couverte de petites épines. Vulve et appareil génital invisibles en raison du mauvais état de conservation du matériel.

Principales mensurations (dans l'ordre: larve du 4ème stade 316 BC; région antérieure 304 BC) : long. 10700 /- ; larg. maximale 400/350; oesophage 1600/1500; ventricule: long. 90/60; larg. 80/80; caecum intestinal 775/750; appendice oesophagien 1275/1700; queue 160 / - ; distance extrémité antérieure - anneau nerveux 350/ 300; - pore excréteur 350/310.

DISCUSSION: les spécimens présentent les caractères du genre *Hysterothylacium*. Aucune espèce du genre n'a été décrite chez les Poissons d'eau douce sud-américains à l'exception de larves du 3ème stade décrites par MORAVEC *et al.* (1993) chez des Poissons de groupes divers; les auteurs supposent que ces larves pourraient appartenir à *H. fortalezae* (Klein, 1973), redécrite par DEARDORFF & OVERSTREET (1981), qui est la seule espèce d'*Hysterothylacium* connue des côtes brésiliennes; nos spécimens se différencient de cette espèce par un caecum intestinal plus long et des ailes labiales pourvues de lobes postérieurs. Bien qu'il renferme quelques espèces parasites de poissons dulçaquicoles, le genre *Hysterothylacium* est essentiellement parasite de Poissons marins; aucun adulte mûr n'ayant été trouvé chez *Platydoras costatus*, nous ne pouvons affirmer que cette espèce est le véritable hôte définitif du parasite et celui-ci peut avoir été apporté dans les eaux douces par un poisson migrateur; la possibilité de développement jusqu'au stade d'adulte immature chez un hôte différent de leur hôte naturel est connue chez les Ascarides (SPRENT 1963).

Raphidascaroides sp.

(fig. 6)

Matériel: 1 femelle juvénile n° MNHN 318 BC (n° de terrain Py 5100) et 2 larves du 4ème stade n° MNHN 309 BC (n° de terrain Py 5102) et n° MHNG 987.489 (n° de terrain Py 5099) (co-parasite: *Hysterothylacium* sp.). Hôte: *Platydoras costatus* (L.), Villeta, prov. Central, 14.11.1987.

DESCRIPTION: - femelle juvénile: corps cylindrique, légèrement aminci à l'extrémité antérieure. Cuticule striée transversalement. Bouche entourée par trois grandes lèvres très allongées, pédonculées, brusquement rétrécies au niveau de leur quart antérieur; ailes labiales dépourvues de lobes dirigés postérieurement; crêtes denticulées absentes; pulpe labiale avec deux lobes antérieurs arrondis; deux papilles doubles sur la lèvre dorsale, une papille double, une papille simple et une amphide sur chaque lèvre latéroventrale; interlabia bien développés, coniques, mesurant la moitié de la longueur des lèvres. Ailes latérales absentes. Pore excréteur au niveau de l'anneau nerveux. Oesophage long, cylindrique. Petit ventricule deux fois plus large que long. Appendice oesophagien court et grêle (1/6 de la longueur de l'oesophage). Caecum intestinal

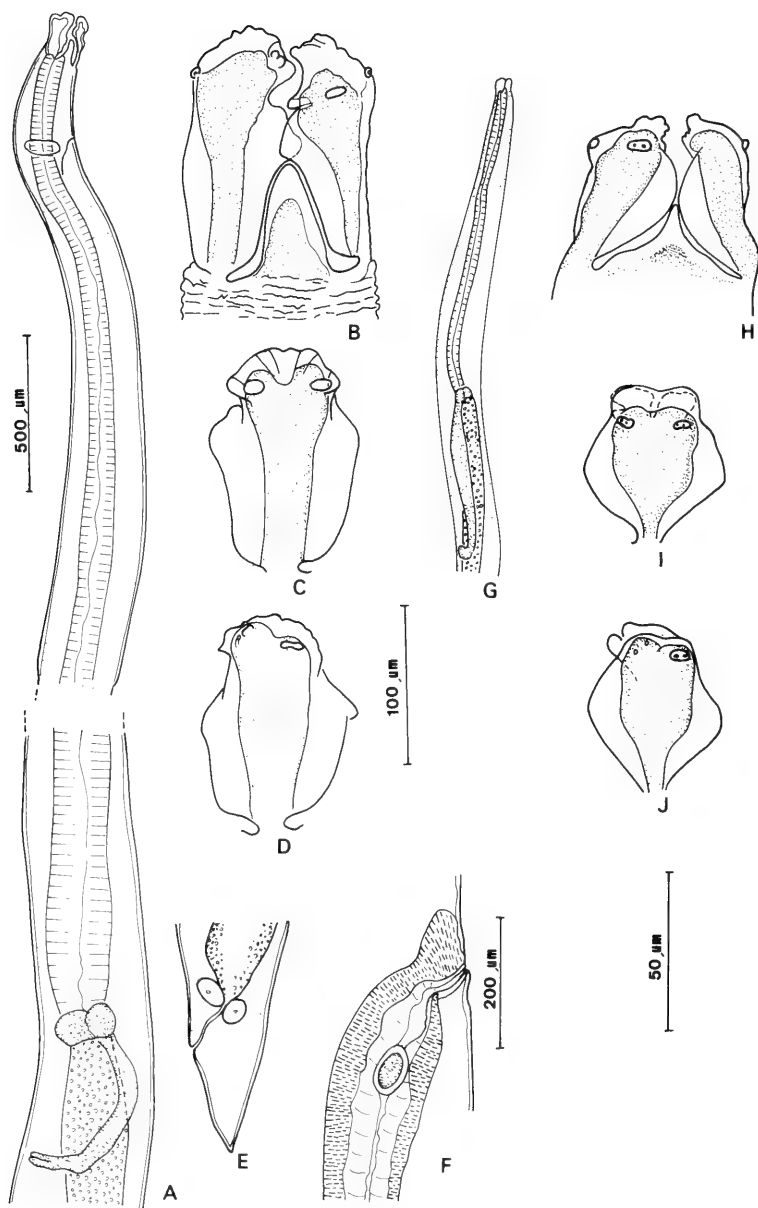


FIG. 6

Raphidascaroides sp. A à F, Femelle juvénile: A, région antérieure, vue latérale; B, extrémité antérieure, vue latérale; C, lèvre dorsale; D, lèvre latéro-ventrale; E, extrémité postérieure, vue latérale; F, région vulvaire; G à J, larve du 4ème stade: G, région antérieure, vue latérale; H, extrémité antérieure, vue latérale; I, lèvre dorsale; J, lèvre latéro-ventrale. Echelles: A,E,G: 500 µm; B,C,D: 100 µm; F: 200 µm; H,I,J: 50 µm.

absent. Queue conique, dépourvue d'épines terminales. Vulve située un peu en avant du tiers antérieur du corps. Long ovéjecteur impair dirigé postérieurement, divisé en deux longs uterus opisthodelphes, contenant quelques oeufs non embryonnés.

Principales mensurations: long. 21000; larg. maximale 500; oesophage 3880; ventricule: long. 90; larg. 170; appendice oesophagien 600; queue 340; distance extrémité antérieure - anneau nerveux 450; - pore excréteur 425; - vulve 6100; ovéjecteur 4000; uterus 4500; oeufs 75/50.

- larves du 4ème stade: elles se différencient de la femelle juvénile par des lèvres moins allongées, un appendice oesophagien relativement plus long par rapport à la longueur de l'oesophage et une queue relativement plus longue.

Principales mensurations: long. 7800/4900; larg. maximale 300/200; oesophage 1260/960; ventricule: long. 70/40; larg. 95/50; appendice oesophagien 550/600; queue 155/160; distance extrémité antérieure - anneau nerveux - /140; - pore excréteur 370/160.

DISCUSSION: par la présence d'interlabia et d'un appendice oesophagien et par l'absence de caecum intestinal, les spécimens se placent dans le genre *Raphidascaroides*. Aucune espèce du genre n'a été signalée jusqu'à présent chez les Poissons d'eau douce sud-américains; comme dans le cas précédent, il n'est pas certain que *Platydoras costatus* soit le véritable hôte définitif du parasite.

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Mikroskopisch-anatomische Untersuchungen der Anorektalregion von Zwergfledermäusen *Pipistrellus pipistrellus* (Schreber, 1774) (Mammalia, Chiroptera)

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Microscopic-anatomical investigations on the ano-rectal region of pipistrelle bats *Pipistrellus pipistrellus* (Schreber, 1774) (Mammalia, Chiroptera).

- Field-studies on the olfactoric communication of Pipistrelle bats are difficult because they are mostly hidden in crevices of houses. An indirect method of investigating is the functional morphology of glands. Scent glands are widespread within the glands entering the integument at mucocutaneous junctions in mammals, which is what we also expected to find in the pipistrelle bat. We chose the ano-rectal region for this study. Five male and five female adult and juvenile Pipistrelle bats found during several months of the year were microscopically investigated.

Both types of ano-rectal glands are more voluminous in males than in females. The sebaceous glands thus show a sexual dimorphism, but no seasonal changes. Their function could not be fully interpreted on the basis of our results. The secretory activity of the proctodaeal glands is less in juveniles than in adults and within the adults the secretory activity is strongest during the mating season in autumn. Sexual dimorphism and seasonal change in the secretory activity of these glands suggest that they are scent glands. Their secretion probably plays an important role during the mating season.

Key-words: *Pipistrellus pipistrellus* - Histology - Morphology.

1. EINLEITUNG

Viele terrestrische Säugetiere haben spezielle Drüsenorgane entwickelt, die Duftstoffe sezernieren. Neben der oft beschriebenen Territoriumsbezeichnung dienen diese Duftstoffe unter anderem der Sexualstimulation, als Orientierungshilfe oder als Alarmsignale und werden gezielt oder zufällig an Objekten der Umgebung, an Artgenossen oder am eigenen Körper aufgetragen oder direkt an die Luft abgegeben (EISENBERG & KLEIMAN 1972, JOHNSON 1973).

In diesem Zusammenhang stellen sich die Fragen, ob und wie aktiv fliegende Säugetiere allfällige Duftmarkierungen anbringen. Zahlreichen mikroanatomischen Untersuchungen, welche zeigen, dass Fledermäuse an verschiedenen Körperregionen Duftdrüsen haben, stehen fragmentarische Freilandbeobachtungen gegenüber. Bei der Zwergfledermaus *Pipistrellus pipistrellus* beispielsweise wurden Analkanaldrüsen mikroskopisch untersucht und Markierungsverhalten in Beziehung zu diesen Drüsen beobachtet. Einerseits fand RAUTHER (1903) zwei verschiedene Drüsentypen, die SCHAFFER (1940) als "Proktodäaldrüse", bzw. "vergrösserte Talgdrüse" bezeichnete. Andererseits landen Männchen während der Paarungszeit in der Nähe ihrer Tages-schlafverstecke auf Bäumen, um vermutlich den Weibchen den Weg in die Paarungs-quartiere zu zeigen (LUNDBERG & GERELL 1986) und das Anfliegen von Wänden bei Gebäudequartieren und gleichzeitige Anbringen von Kot bezeichnete GRIMMBERGER (1983) als "Kotkleben".

Ziel der vorliegenden Arbeit ist es, anhand von mikroskopischen Untersuchungen abzuklären, ob die Drüsen in der Anorektalregion von Zwergfledermäusen Duftdrüsen sind und ob geschlechtsspezifische und saisonale Unterschiede vorhanden sind, die auf die Funktion dieser Drüsen hinweisen könnten.

2. MATERIAL UND METHODEN

Für die grobmorphologischen und histologischen Untersuchungen wurden 10 Zwergfledermäuse verwendet (Tab. 1.). Der mit den umliegenden Organen heraus-sezierte Analkanal wurde nach den herkömmlichen Methoden zu lückenlosen Serien von 7-10 μ dicken Paraffinschnitten weiterverarbeitet und mit Haemalaun-Eosin und Goldner (ROMEIS 1968) gefärbt. Das Alter und der reproduktive Zustand der unter-suchten Zwergfledermäuse wurde in Anlehnung an RACEY (1974) beurteilt. Frisch flügge Tiere, deren Epiphysen der Fingerglieder noch nicht vollständig verknöchert waren, konnten von Adulten unterschieden werden. Sexuell reife und sexuell aktive Männchen wurden an der Spermatogenese in den Hoden, bzw. am Vorhandensein von Spermien in den Nebenhoden erkannt. Weibchen, die mindestens einmal ein Junges gesäugt hatten (Zitzen abgeflacht) konnten von solchen unterschieden werden, die noch nie ein Junges gesäugt hatten. Der saisonale Aktivitätszustand der Drüsen in der Anorektalregion wurde auf Grund verschiedener Merkmale untersucht (Tab. 1.). Die Querschnitte wurden in vier Sektoren unterteilt (ventral, dorsal, zweimal lateral). Für jeden Querschnitt und jeden Sektor wurde das Vorhandensein der entsprechenden Drüse notiert, mit der Schnittdicke multipliziert und durch die Anzahl Sektoren geteilt. Dadurch konnte die Längenausdehnung des Proktodäal- (PDB), bzw. des Talg-drüsenbereichs (TDB) berechnet werden. Aus dem mittleren Teil jedes Bereiches wurden an drei Schnitten die Flächen der Drüsen auf mm-Papier ausgezählt und der Durchschnitt als Flächenmass des Proktodäal- (PDB), bzw. des Talgdrüsenbereichs (TDB) verwendet. Als weitere Kriterien für den Aktivitätszustand diente bei beiden Drüsentypen das Vorhandensein von Sekret im Lumen und im Ausführgang, bei den Proktodäaldrüsen der durchschnittliche Durchmesser der Endstücke, und der Grad der Erweiterung des Ausführganges.

TAB. 1

Untersuchte Zwergfledermäuse und Aktivität der Proktodäal- und Talgdrüsen nach Geschlecht und Monat. Geschlecht: männlich (1), weiblich (2); reproduktiver Zustand Männchen: frisch flügge und sexuelle Reife noch nicht erlangt (a), adult und sexuell inaktiv (b); reproduktiver Zustand Weibchen: adult und noch nie ein Junges gesäugt (a), adult und mindestens einmal ein Junges gesäugt (b); Proktodäaldrüsenbereich (PDB); Talgdrüsenbereich (TDB); Merkmal nicht erhoben (x); Erweiterung der Ausführungsgänge schwach (sch), mittel (m), stark (st)

Sammlungsnummer	3815	3934	3554	4206	4487	3819	3930	1549	2892	2997
Geschlecht	1	1	1	1	1	2	2	2	2	2
reproduktiver Zustand	b	b	a	a	b	a	a	b	b	a
Monat	IV	VI	VIII	VIII	XI	IV	VI	VII	IX	XII
Proktodäaldrüsen										
Sekret in Endstücken u. Ausführungsgängen	+	+	-	+	+	+	+	+	+	-
Erweiterung der Ausführungsgänge	m	m	sch	m	sch	m	m	sch	st	sch
Endstückdurchmesser in μ	27,5	26	23	23	25	25	28	25	34,5	20,5
Längenausdehnung des PDB in μ	726	663	x	x	682	x	552	x	722	580
Flächeneinheiten des PDB	4425	6817	x	x	3408	x	3942	x	5990	3617
Talgdrüsen										
Sekret in Ausführungsgängen	+	+	+	+	+	+	+	+	+	+
Längenausdehnung des TDB in μ	527	318	x	x	464	x	312	x	301	303
Flächeneinheiten des TDB	1908	1650	x	x	1992	x	958	x	1662	2058

3. RESULTATE

Der Analkanal hat bei den untersuchten Zwergfledermäusen je eine Länge von ca. 2 mm und ist in drei Bereiche unterteilbar. Die Schleimhaut der kranialen Zona columnaris ist in Längsfalten angeordnet. Während die Uebergangszone zur Rektalschleimhaut Becherzellen im Epithel aufweist, ist kaudal ein mehrschichtiges Plattenepithel vorhanden. Die Schleimhaut der Zona intermedia ist eher glatt. Hier ist ein dickes, unverhorntes, mehrschichtiges Plattenepithel vorhanden. Alle Proktodäaldrüsen münden in diese Zone. Sie sind rund um den Analkanal angeordnet und erstrecken sich in die beidseits benachbarten Zonen. Die Ausführungsgänge, deren Lumen eine beträchtliche Weite einnehmen können, ziehen jeweils in leicht geschlängeltem Verlauf peripher nach aussen. Mehrere verzweigte Streifenstücke münden in einen Ausführungsgang und enden ihrerseits in sekretproduzierenden Drüsenendstücken (Abb. 1.a-c). Die Zona cutanea stellt als äusserster Abschnitt des Analkanals den Uebergang zur Körperhaut dar. Hier mündet in jeden Haarbalg eine vergrösserte Talgdrüse (Abb. 1.d). Die

Weibchen haben weniger Drüsen, die insgesamt einen kleineren Analkanalbereich einnehmen, als die Männchen. Während die Talgdrüsen bei beiden Geschlechtern das ganze Jahr hindurch ähnlich aktiv sind, ist die Aktivität der Proktodäaldrüsen saisonalen Schwankungen unterworfen. Extrem aktive Proktodäaldrüsen haben das paarungsbereite Weibchen aus dem September und das Männchen aus dem Juni. Schwach aktive Proktodäaldrüsen haben beide Geschlechter in den Monaten November und Dezember, das frisch flügge Männchen aus dem August und das adulte Weibchen aus dem Juli (Tab. 1.).

4. DISKUSSION

Der von vielen anderen Säugetieren bereits bekannte Sexualdimorphismus bei den Drüsen der Anorektalregion konnte hier erstmals für die Zwergfledermaus nachgewiesen werden. Zusätzlich wurde eine saisonale Aenderung der Aktivität der Proktodäaldrüsen bei beiden Geschlechtern festgestellt. Die grösste Drüsenaktivität ist bei den Weibchen während der herbstlichen Paarungszeit, und auch bei den Männchen dürfte dies der Fall sein, denn trotz fehlendem Präparat aus dieser Jahreszeit, deuten die bereits während der Spermatogenese deutlich aktiveren Drüsen auf eine Zunahme der Sekretion in der Paarungszeit hin. Wie bei den a-Drüsen im Schnauzenintegument (HAFFNER 1987), ist die Drüsensaktivität im Winter gedrosselt. Die Sekretproduktion der Talgdrüsen scheint hingegen jahreszeitlich unabhängig konstant zu sein. Dass die Talgdrüsensekrete lediglich eine Schutzfunktion für die Anorektalregion ausüben (RAUTHER 1903), erscheint auf Grund des festgestellten Sexualdimorphismus zugunsten der kleineren Männchen eher unwahrscheinlich. Ob ihre Sekrete jedoch als Träger der von den Proktodäaldrüsen sezernierten Duftstoffe im Sinne von STARCK (1982) dienen oder selber Duftstoffe enthalten (BEREITER-HAHN *et al.* 1986), kann anhand der vorliegenden Untersuchung nicht belegt werden.

Die saisonalen Schwankungen mit einem Aktivitätsmaximum in der Paarungszeit und der Geschlechtsdimorphismus bei den Proktodäaldrüsen hingegen deuten darauf hin, dass es sich bei diesen Drüsen um Duftdrüsen handelt. Wie MEYER (1976) für andere Säugetiere und BUCHLER (1980) für *Myotis lucifugus* beschrieb, dürften die austretenden Sekrete auf die passierenden Exkreme, die als Vehikel für die Duftstoffe dienen, abgegeben werden. Dadurch kann auch die Vermutung von LUNDBERG (1989), welche das kurzfristige Landen männlicher Zwergfledermäuse während der Paarungszeit auf exponierten Stellen in Zusammenhang mit Markierungsverhalten brachte, bekräftigt werden.

ZUSAMMENFASSUNG

Feldstudien zur olfaktorischen Kommunikation von Zwergfledermäusen sind schwierig durchzuführen, da diese Tiere tagsüber meist versteckt in Spalten und Ritzen an Gebäuden leben. Eine indirekte Untersuchungsmethode stellt die funktionsmorphologische Untersuchung von Drüsen dar. Duftdrüsen sind an mukokutanen Uebergängen bei Säugetieren weitverbreitet, was wir auch für die Zwergfledermaus vermuteten. Wir wählten die Anorektalregion für diese Untersuchung aus und stellten

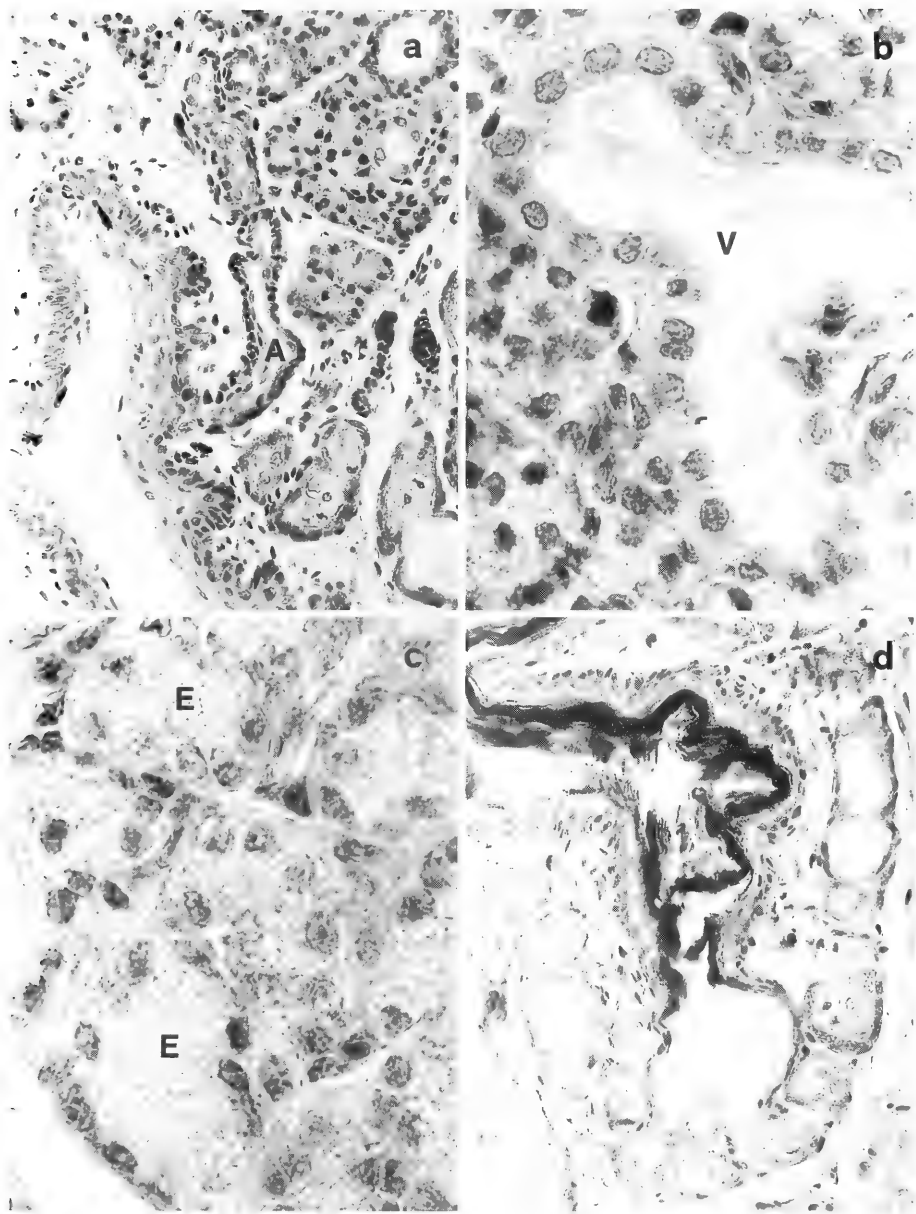


ABB. 1

Mikroanatomie der Proktodäaldrüsen (a-c) und der Talgdrüsen (d) im Analkanal. a: Ausführungsgang (A) mit zweischichtigem Epithel (ca. 280x), b: Streifenstücke mit Verzweigung (V) (ca. 840x), c: Endstücke (E) (ca. 950x), d: vergrößerte Talgdrüse (ca. 260x).

lückenlose histologische Präparatserien her von je fünf männlichen und weiblichen adulten und juvenilen Zwergfledermäusen aus verschiedenen Fundmonaten.

Beide Typen der Analkanaldrüsen sind bei den Männchen sowohl absolut wie auch relativ voluminöser als bei den Weibchen. Die Talgdrüsen weisen somit einen Sexualdimorphismus, jedoch keine saisonalen Veränderungen auf. Ihre Funktion konnte auf Grund der vorliegenden Resultate nicht eindeutig interpretiert werden. Die sekretorische Aktivität der Proktodäaldrüsen ist bei Jungtieren gering und bei den Erwachsenen während der herbstlichen Paarungszeit am grössten. Der Sexualdimorphismus und die saisonalen Aenderungen in der sekretorischen Aktivität der Proktodäaldrüsen weisen darauf hin, dass es sich um Duftdrüsen handelt. Ihre Sekrete spielen wahrscheinlich in der Paarungszeit, z.B. beim auffälligen Verhalten der Männchen in der Umgebung ihrer Balzquartiere, eine besonders wichtige Rolle.

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Chilioesthetus ernstjuengeri* sp. n., der erste Gattungsvertreter aus Australien (Coleoptera, Styphlinidae)

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Chilioesthetus ernstjuengeri sp. n., the first *Chilioesthetus* Saiz from Australia (Coleoptera, Styphlinidae). - *Chilioesthetus ernstjuengeri* sp. n. is described from Queensland, Australia. This species is the first example for transantarctic distribution in the Euaesthetinae.

Key-words: Coleoptera - Styphlinidae - *Chilioesthetus* - Australia - Transantarctic distribution.

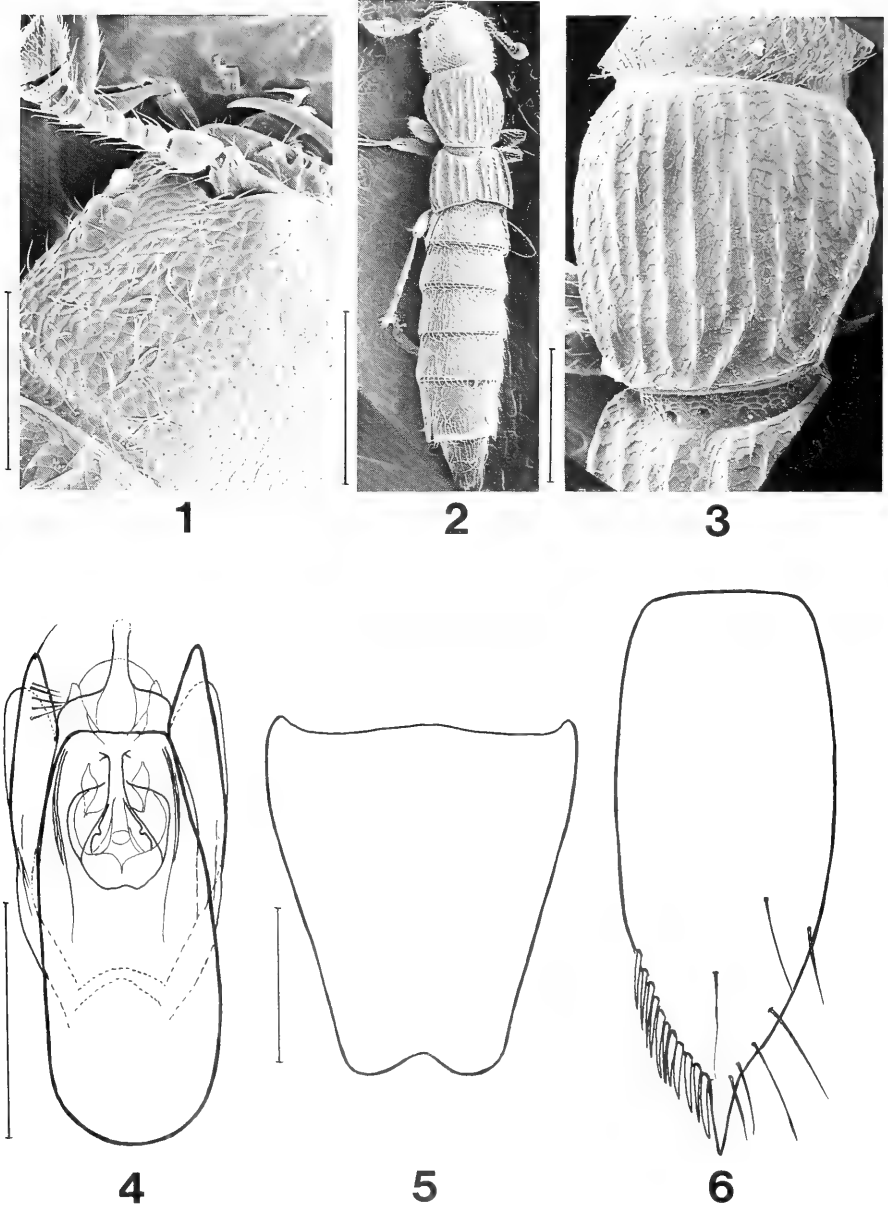
EINLEITUNG

In dieser Arbeit wird eine neue Art der Gattung *Chilioesthetus* Saiz beschrieben, die insofern bemerkenswert ist, als sie das erste Beispiel für transantarktische Verbreitung einer Euaesthetinengattung bildet. Schon 1978 habe ich auf die phylogenetische Nähe des Genus *Tasmanosthetus* Putz zu *Chilioesthetus* Saiz hingewiesen (Putz 1988: 118) und auf die gondwanische Herkunft aufmerksam gemacht. Die hier vorgelegte neue Art bestätigt meine damals geäußerten Vermutungen. Zum transantarktischen Verbreitungstyp vgl. ZWICK, 1977 und NEWTON, 1985.

Es ist mir eine besondere Freude, diese bemerkenswerte neue Spezies dem deutschen Schriftsteller und Koleopterologen Ernst Jünger zu seinem hundertsten Geburtstag herzlich zu widmen. Immer wieder hat er in seinen zahlreichen Werken die Natur, vor allem auch die Insekten als Metapher gedeutet und damit erfüllt, was Goethe in seinem "Epirrhema" so ausdrückt:

Müset im Naturbetrachten
Immer eins wie alles achten:
Nichts ist drinnen, nichts ist draußen;
Denn was innen, das ist außen.
So ergreift ohne Säumnis
Heilig öffentlich Geheimnis.

* 75. Beitrag zur Kenntnis der Euaesthetinen
Manuskript angenommen am 07.12.1994.



Figs 1-6

Chilioesthetus ernstjuengeri sp. n. (Paratype): Teil des Kopfes, leicht gekippt (1), Totalansicht (2), Pronotum und Teile von Kopf und Elytren, etwas gekippt (3). Maßstab: 1, 3 = 0,1 mm, 2 = 0,5 mm. Ventralansicht des Aedoeagus (4), 8. Sternit (5) und 9. Sternit (6) des Männchens (Borsten z.T. weggelassen). - Maßstab = 0,1 mm (4 = 6). - Fotos von Dr. O. Betz (Kiel), dem dafür auch an dieser Stelle herzlich gedankt sei.

Chilioesthetus ernstjuengeri sp. n.

(Fig. 1-3)

Apter, mikrophthalm, rötlichbraun, Kopf matt, Rest des Körpers schwach schimmernd. Kopf dicht genetzt mit zahlreichen Sensillenporen, Labrum mit 12 vorderen Zähnen; Pronotum und Elytren längsrippig skulptiert, Oberfläche zwischen den Rippen genetzt; Abdomen dicht ananasschuppig genetzt. Fühler, Taster und Beine gelblich. Behaarung fein, mäßig dicht.

Länge: 1,2 - 1,6 mm (Vorderkörperlänge: 0,6 mm).

♀ - Holotypus: Australien: Queensland, Mt. Lewis, 1060 m, 16034' S, 145017' E, rain-forest, 20.VI.1971, ANIC Berlese 317 (Mus. Comp. Zool., Harvard Univ., Cambridge, Mass.).

Paratypen: 1♀, 1♂: wie Holotypus: das ♂ vollständig zerlegt, die Teile eingebettet in Euparal auf zwei Celluloidplättchen und einem Mikroskop-Objekträger, das o vergoldet für REM-Aufnahme (MCZH und coll. Puthz in Mus. his. nat. Genf).

Proportionsmaße des Holotypus: Kopfbreite: 26; Kopflänge (Labrum bis Halsabschnürung): 22; Augenabstand: 22; Augenlänge: 5; Schläfenlänge: 7,5; Wangenlänge: 5; Pronotumbreite: 28; Pronotumlänge: 27; Elytrenbreite: 28,5; Elytrenlänge: 21; Nahtlänge: 15.

MÄNNCHEN: 8. Tergit am Hinterrand jederseits flach konkav ausgebuchtet, die Mitte stumpf vorgezogen. 8. Sternit (Fig. 5). 9. Sternit (Fig. 6). A e d o e a g u s (Fig. 4), Parameren in zwei Längsäste gespalten.

WEIBCHEN: 8. Sternit apikal abgerundet. Valvifera apikal spitz.

Die neue Art unterscheidet sich von allen bisher (nur aus Chile) bekannten *Chilioesthetus*-Arten sofort durch ihre furchige Oberflächenskulptur und durch den Aedoeagus.

Ich habe anfangs angenommen, es handele sich bei diesen australischen Käfern um einen abweichenden *Austroesthetus* oder eine neue *Tasmanosthetus*-Art. Von *Austroesthetus* Oke unterscheidet sie sich aber sofort durch viel kleinere Augen und das vorn jederseits abgerundete Labium. NEWTON hat 1985 geäußert, daß *Chilioesthetus* und *Austroesthetus* "should probably be combined" (p. 205), dies ist jedoch wegen der erwähnten Unterschiede nicht möglich. Von *Tasmanosthetus* trennt man die neue Art durch ihre enge, zweigliedrige Fühlerkeule und seitlich gerandetes 3. Abdominalsegment. Wenn auch der Vorderrand ihres Prosternums nur schwach crenuliert ist, so kann ich doch keine stringenten Unterschiede zu chilenischen Gattungsvertretern finden. Auch die rechte Mandibel trägt - wie bei chilenischen Arten - einen kleinen, zusätzlichen, dritten Zahn.

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Revision of the genus *Sternocoelis* Lewis, 1888 (Coleoptera: Histeridae), with a proposed phylogeny

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Revision of the genus *Sternocoelis* Lewis, 1888 (Coleoptera: Histeridae), with a proposed phylogeny.

- Twenty six species of *Sternocoelis* Lewis are currently recognized and all occur in the Mediterranean region. *Sternocoelis espadaleri* n. sp. is described from Morocco. The structure of the pronotum, elytra, prosternum and legs were found to be particularly diagnostic. The following new synonyms are proposed: *Sternocoelis ovalis*, 1900 syn. nov. of *S. viaticus* Lewis, 1892; *S. mauritanicus* Lewis, 1888 syn. nov. of *S. fuscus* (Schmidt, 1888); *S. aureopilosus* Escalera, 1921 syn. nov. of *S. fuscus* (Schmidt, 1888); *S. variolosus* Théry, 1921 syn. nov. of *S. alluaudi* Théry, 1921; *S. loustali* Kocher, 1956 syn. nov. of *S. alluaudi* Théry, 1921; *S. politus* (Schmidt, 1888) syn. nov. of *S. bedeli* (Lewis, 1884); *S. cancer* Lewis, 1888 syn. nov. of *S. bedeli* (Lewis, 1884), *S. extructisternum* Lewis, 1888 syn. nov. of *S. bedeli* (Lewis, 1884); *S. pectoralis* Lewis, 1888 syn. nov. of *S. bedeli* (Lewis, 1884); *S. sedilloti* Lewis, 1889 syn. nov. of *S. bedeli* (Lewis, 1884); *S. bonnairei* (Schmidt, 1888) syn. nov. of *S. setulosus* (Reitter, 1872); *S. walkeri* Lewis, 1888 syn. nov. of *S. setulosus* (Reitter, 1872); *S. fulvus* Lewis, 1888 syn. nov. of *S. setulosus* (Reitter, 1872); *S. cancriformis* Escalera, 1921 syn. nov. of *S. slaoui* Théry, 1921.

The lectotypes and paralectotypes of the following taxa are designated: *Hetaerius lewisi* Reitter, 1883, *H. pluristriatus* Fairmaire, 1877, *H. cavis-ternus* Marseul, 1862, *H. bedeli* Lewis, 1884, *H. politus* Schmidt, 1888, *H. bonnairei* Schmidt, 1888, *H. hispanus* Rosenhauer, 1856, *Haeterius marseulii* Brisout de Barneville, 1866, *Sternocoelis otini* Peyerimhoff, 1949, *S. marginalis* Normand, 1915, *S. laeviodorsis* var. *major* Pic, 1905, *S. laeviodorsis* var. *semiopacus* Normand, 1915, *S. viaticus* Lewis, 1892, *S. vaucheri* Lewis, 1896, *S. aureopilosus* Escalera, 1921, *S. alluaudi* Théry, 1921, *S. cancer* Lewis, 1888, *S. walkeri* Lewis, 1888, *S. fulvus* Lewis, 1888 and *S. cancriformis* Escalera, 1921.

A putative phylogenetic tree is proposed and the zoogeography is also discussed.

Key-words: Coleoptera - Histeridae - *Sternocoelis* - Revision - Phylogeny.

INTRODUCTION

The genus *Sternocoelis* Lewis is a small genus of myrmecophilous histerids distributed in the Mediterranean area (MAZUR, 1984). This genus was established by LEWIS (1888a) to include the species of *Hetaerius* Erichson with a widely and deeply excavated meso- and metasternum. The other genera of Palearctic Hetaeriinae are *Eretmotus* Lacordaire and *Satrapes* Schmidt.

The genus *Sternocoelis* can be readily distinguished from other Palearctic Hetaeriinae by the excavated meso-metasternum. It otherwise resembles the related genus *Hetaerius*.

SCHMIDT (1885c) published a key to the species of *Hetaerius* including several species nowadays included in the genus *Sternocoelis*. Recently (YÉLAMOS, 1993) published a work on the Iberian species of *Sternocoelis*. Historically there have been many species, descriptions of species, systematic changes and new geographical records: LEWIS, 1884, 1887, 1888a, 1889, 1892b, 1894, 1896 and 1900; SCHMIDT; 1885a, 1885b and 1888; PIC, 1905, 1910, 1911 and 1937; FAIRMAIRE, 1876, 1877 and 1883; BICKHARDT, 1913 and 1917; ESCALERA, 1921 and 1929; KOCHER, 1956 and 1958; MARSEUL, 1857 and 1862; MOTSCHULSKY, 1937 and 1858; REITTER, 1872 and 1883; BRISOUT DE BARNEVILLE, 1866; COBOS, 1949; ESPAÑOL, 1970; KRYZHANOVSKIJ & REICHARDT, 1976; LUCAS, 1855; MENOZZI, 1942; NORMAND, 1915; PEYERIMHOFF, 1949; ROSENHAUER, 1856; RAGUSA, 1882; SCHLEICHER, 1930; THÉRY, 1921. Other works on their general biology are: LEWIS, 1888b, 1891 and 1892a; WALKER, 1889. HELAVA *et al.* (1985) published an extensive study on the American Hetaeriinae, including the Nearctic species of *Hetaerius*.

YÉLAMOS (1992) published a revision of the genus *Eretmotus* as a preliminary step before doing it so on the close *Sternocoelis*.

The present work would not have been possible without loans from several Museums. All type series have been studied with the exception of *Sternocoelis loustali* Kocher, 1956, that was not loaned by the Institut Scientifique Chérifien from Rabat, and of *Hetaerius grandis* Reitter, 1883 and *Sternocoelis sulcaticollis* Pic, 1937 both not found in the European Museums. Therefore, the study of these species is based on their descriptions.

ABBREVIATIONS

- DEI: Deutsches Entomologisches Institut, Eberswalde, Germany.
- EEZA: Estación Experimental de Zonas Áridas, Almería, Spain.
- JM: Josep Muñoz, private collection, Girona, Catalonia, Spain.
- MHNG: Musée d'Histoire Naturelle, Genève, Switzerland.
- MNCN: Museo Nacional de Ciencias Naturales, Madrid, Spain.
- MNHN: Muséum National d'Histoire Naturelle, Paris, France.
- MNHU: Museum für Naturkunde der Humboldt-Universität, Berlin, Germany.
- MZ: Museu de Zoologia, Barcelona, Catalonia, Spain.
- NHML: The Natural History Museum, London, United Kingdom.

NHMW: Naturhistorisches Museum, Wien, Austria.

TM: Termesztudományi Múzeum, Budapest, Hungary.

TY: Tomàs Yélamos, private collection, Barcelona, Catalonia, Spain.

ZM: Zoologisk Museum, København, Denmark.

ZMMLSU: Zoological Museum Moscow Lomonosov State University, Russia.

Subfamily HETAERIINAE Marseul, 1857

Hétériens Marseul, 1857. *Ann. Soc. Ent. Fr.*, (3)5: 148.

Sternocoelis Lewis, 1888

Sternocoelis Lewis, 1888a: 144.

Type species: *Hetaerius acutangulus* Lewis, 1887. Designated by Bickhardt, 1917: 257.

Form globose, oval, convex; setose; length between 1.3-2.8 mm.

Frons with lateral margins carinate, reaching the epistoma; labrum with apical margin truncate; antennal scape strongly enlarged (fig. 24); antennal club cylindrical, lacking annular rings and heavily sclerotized except at truncate apex (photographs 1 and 2).

Pronotum with anterior angles rather broadly, obliquely truncate, elevated; disc convex; anterior angles sometimes expanded, accompanied by a depression near the base of the third elytral stria. Elytra with dorsal striae 1-3 usually present and slightly impressed; stria 4 present only in one species (*S. pluristriatus*); dorsal striae sometimes indicated by rows of setae; external subhumeral stria sinuate, complete, cariniform; marginal stria long, cariniform, usually joined medially with external subhumeral stria (figs. 25 and 26).

Pygidium wide and long in relation to elytra. Pygidium short and convex. Prosternum with keel having very diverse morphology; inner prosternal striae usually strong, convergent or not in front, sometimes evanescent; posterior margin broadly, roundly emarginate, expanded at sides; lobe separated from keel by a variably impressed suture, sometimes by a deep depression; lobe truncate sinuate or divided into two portions. Mesosternum produced in front to fit prosternal emargination; marginal stria fine; lateral foveae usually deep (excretor orifices) situated next to mesocoxae (fig. 27); meso-metasternum deeply excavate; meso-metasternal suture slight. Metasternum with postcoxal and three lateral striae (outer, medial, inner) present (figs. 51-53).

First abdominal sternite with two postcoxal striae.

Legs variably long and expanded.

Male 8th abdominal segment wide and lightly sclerotized; spiculum gastrale Y-shaped; aedeagus with basal piece short; parameres wide and long, distally separated.

BIOLOGY

Little has been published on the biology of *Sternocoelis*. Larvae and pupae are unknown. LEWIS (1888b) reported some interesting biological observation during

field studies in Spain, Morocco and Algeria. These beetles dwell in clay soils, always within the nests of several ant genera (*Aphaenogaster*, *Cataglyphis*, *Messor* and *Formica*). No species specificity was detected among the ant hosts. However most specimens were found in the nests of several species of *Aphaenogaster*. *Sternocoelis* feeds on larvae and dead adult ants. Within the nest they frequent the ant brood chambers when brood is present. During cool wet weather, both ant's brood and the *Sternocoelis* were found under medium-sized stones (between 20-40 cm). In hot, dry weather, these beetles tend to be found deep within the ant nest.

According to Lewis, ants are unable to grasp *Sternocoelis* with their mandibles due to the hard, smooth nature of their cuticle. Thus, the ants treat these beetles with indifference. Some specimens of *Sternocoelis* were observed clinging to the abdomen of ants with their legs and thus ride on their backs into lower galleries of the nest.

In temperate lowlands *Sternocoelis* is active from winter to the beginning of spring. At higher elevations they appear to be active from midspring up to the beginning summer. Beetle activity was recorded from November up to June, with a few specimens found per ant nest.

KEY TO THE SPECIES

- 1 Mesosternum lacking deep lateral foveae near mesocoxae¹. 2
- Mesosternum with deep lateral foveae near mesocoxae 15
- 2 Sides of pronotum clearly separated from disc by a complete oblique impression, explanate. 3
- Sides of pronotum not completely separated from disc, usually with short basal and apical impressions. 7
- 3 Prosternal lobe at lower level than keel, with an abrupt transition between both parts. 4
- Prosternal lobe situated at slightly lower level, equal to or superior to keel. . . 5
- 4 Pronotum and metasternum coarsely and densely punctate; prosternal keel with inner striae complete (but fine), subparallel, outer striae evanescent (fig. 37); first dorsal striae slightly surpassing middle; elytral epipleurae with two irregular striae; tibiae more expanded (fig. 59). *S. grandis*
- Pronotum and metasternum finely and sparsely punctate; prosternal keel with inner striae fine, short, medially arcuate, the outer stria distinct (fig. 34); first dorsal striae complete; elytral epipleurae without striae; tibiae less expanded (fig. 57). *S. otini*
- 5 Prosternal lobe distinctly at weakly superior level of prosternal keel; prosternal keel narrow and long (fig. 35). *S. marginalis*

¹ Several specimens of *S. fuscus* have incipient lateral foveae in the mesosternum, which are sometimes difficult to see; these specimens might be confused with *S. incisus*, which can be distinguished by the different morphology of prosternum and mesosternum.

- Prosternal lobe distinctly at lower level of keel; prosternal keel wide and short (figs 36 and 38). 6
- 6 Prosternal lobe not emarginate (fig. 36); prosternal keel strongly rugose and wide, with inner striae evanescent. *S. laevidorsis*
- Prosternal lobe emarginate (fig. 38), depressed in the middle; prosternal keel only slightly rugose and narrow, with inner striae reaching 2/3 total length. *S. rugosus*
- 7 Prosternal lobe clearly below level of keel, with a strong demarcation between both parts (fig. 32). *S. puberulus*
- Prosternal lobe at slightly below, at same level or slightly above level of keel. 8
- 8 Prosternal lobe deeply emarginate, divided into two parts, separated from keel by a deep depression (fig. 49); sides of pronotum parallel (fig. 22), rounded, without marginal stria; elytra without striae; legs narrow and elongate, not expanded (fig. 67). *S. comosellus*
- Prosternal lobe variably emarginate, never with a deep emargination or divided, sometimes separated from keel by a slight depression, sides of pronotum not parallel, or rounded, with marginal stria variably impressed; elytra with striae; tibiae usually very expanded, length variable. . 9
- 9 Elytra with the first three dorsal striae complete or slightly abbreviated, the fourth obsolete or reduced on the distal half; three metasternal striae very long, the inner two striae approaching the metacoxae (fig. 52); pronotal disc and median part of elytra strongly convex. *S. merkliei*
- Elytra usually with complete first dorsal striae, and with a basal remnant of the third stria; three metasternal striae of varying length; pronotal disc and median part of elytra not strongly convex. 10
- 10 Prosternal lobe deflexed, obliquely oriented in relation to plane of keel (fig. 39); meso-metasternal excavation deep. *S. fuscus*
- Prosternal lobe either at same level as central part of keel or slightly sloping; meso-metasternal excavation shallow. 11
- 11 Prosternal lobe at a same level as central part of keel (fig. 28), emarginate, with sides more deflexed than keel; prosternal keel very wide; upper side of body with long aligned setae. *S. viaticus*
- Prosternal lobe sloping in relation to keel, always at lower level; prosternal keel narrow (fig. 31); upper side of body with setae of diverse morphology. 12
- 12 Inner prosternal striae fine, indistinct by rugosity, mainly visible distally, not clearly joined anteriorly; upper side of body with short setae, not aligned, markedly and densely punctate; prosternal lobe emarginate; meso-metasternal excavation deep. 13
- Inner prosternal striae distinct, joined anteriorly; upper side of body with long aligned setae, finely and sparsely punctate; prosternal lobe not emarginate; meso-metasternal excavation shallow. 14

- 13 Inner prosternal striae not subparallel (fig. 31), approaching, with a short median part of outer striae; prosternal lobe clearly emarginate; inner metasternal stria reaching only 1/3 length of metasternum; epipleurae with a trace of stria. *S. diversepunctatus*
- Inner prosternal striae subparallel (fig. 30), very distant, without short part of outer striae; prosternal lobe slightly emarginate; inner metasternal stria reaching between 1/2-2/3 length of metasternum; epipleurae without stria. *S. lewisi*
- 14 Anterior pronotal angles very produced, flattened; pronotum with sparse setigerous pores; elytra weakly broad; meso-metasternal excavation deep; metasternum without distinct part of inner stria; discs of both metasternum and first abdominal sternite punctate. *S. marseulii*
- Anterior pronotal angles weakly expanded, not flattened; pronotum with dense setigerous pores; elytra very broad; meso-metasternal excavation extremely shallow; metasternum with a short and distinct inner stria remnant; discs of both metasternum and first abdominal sternite smooth. *S. vaucheri*
- 15 Prosternal lobe deeply emarginate or divided into two parts (fig. 50); sides of pronotum rounded, parallel and lacking marginal stria; legs very long, not expanded (fig. 68). *S. espadaleri*
- Prosternal lobe bisinuate, not deeply emarginate; sides of pronotum with marginal stria, occasionally straight or parallel; leg morphology variable. 16
- 16 Prosternal keel and lobe separated by a deep depression (fig. 41); meso- and metatibiae very expanded (fig. 61); inner prosternal striae with a wide medial projection (fig. 41). 17
- Prosternal keel and lobe not separated by a deep depression. sometimes with a shallow depression or keel and lobe on the same level; meso- and metatibiae variably enlarged; when there is a depression between lobe and keel, then legs very long, not enlarged and lacking medial projections of inner prosternal striae. 19
- 17 Inner metasternal stria very short; lateral mesosternal foveae broad and deep. *S. alluaudi*
- Inner metasternal stria very long and reaching metacoxae; lateral mesosternal foveae variable. 18
- 18 Posterior pronotal angles abruptly produced (fig. 13); sides of pronotum parallel; pronotum very densely punctate, mainly at sides and apical half; body covered with long and dense setae on sides and posterior half; inner prosternal striae with wide and laterally expanded medial projections (fig. 41); protibiae stout and expanded (fig. 61); mesosternal foveae broad and very deep; length 2.2-2.5 mm. *S. acutangulus*
- Posterior pronotal angles gradually produced (fig. 11); sides of pronotum not parallel; pronotum less densely punctate; body covered by short, broad and dense setae on entire surface; inner prosternal striae

- with fine medial projections extending laterally (fig. 40); protibiae expanded; mesosternal foveae narrow, elongate and shallow; length 1.3-1.7 mm. *S. incisus*
- 19 Inner prosternal striae with a distinct projection on anterior 2/3; prosternal keel very rugose; medial part of prosternal keel at a same level as the not deflexed poststernal lobe; legs short and very expanded; length of metatibiae less than half total length of body; maximum expansion metatibiae equal to half length of body. 20
- Inner prosternal striae either straight or sinuate, lacking a distinct anterior projection; prosternal keel either smooth or punctate but not rugose; medial part of prosternal keel not at same level and deflexed; legs long, less expanded; length of metatibiae equal to or more than half total length of body; maximum expansion of metatibiae equal to 1/3 length of body 22
- 20 Elytra with an arcuate basal part of fourth dorsal stria; posterior pronotal angles not produced (fig. 14). *S. pluristriatus*
- Elytra without a trace of fourth dorsal striae; posterior pronotal angles variably produced (figs. 15 and 16). 21
- 21 Pronotum, elytra, propygidium and pygidium covered with long, yellow recumbent setae; disc of pronotum and elytra with setigerous pores and sparse, fine punctures, slightly more dense on elytra; elytra subparallel, slightly enlarged at shoulders; disc of metasternum with a variably deep impression on both sides. *S. punctulatus*
- Pronotum, elytra, propygidium and pygidium covered with erect yellow setae of median length (in some specimens there are only erected setae on sides, because the other lie down); upper side of body with large punctures of variable density, always with setigerous pores; elytra strongly enlarged, not subparallel; metasternal disc without lateral impressions. *S. bedeli*
- 22 Prosternal lobe either at same level as keel or separated by a shallow depression (fig. 45); metasternum with inner stria well impressed and nearly reaching metacoxae; mesotibiae strongly expanded medially; metatibiae long (length of metatibiae/total length body = 0.46-0.52), with medial triangular expansion (maximum width between 1/3-1/4 of tibial length), basal half narrower than distal half; body covered with long, erect setae as well as additional microsetae. *S. setulosus*
- Prosternal lobe clearly more prominent than keel or separated from keel by a distinct impression; metasternum with both inner striae less impressed and not reaching metacoxae; mesotibiae gradually expanded in distal half; metatibiae longer (length of metatibia/total length body = 0.58-0.75) and slender, not triangular (maximum width clearly lower than 1/3 length); pubescence variable. 23
- 23 Inner prosternal striae obsolete, at same level as outer ones; prosternal lobe and keel without a depression between them (fig. 44); meso- and

- metatibiae slightly expanded medially (fig. 62); upper side body surface with mixture of very long and very short setae. *S. atlantis*
- Inner prosternal striae distinct and elevated above outer ones; prosternal lobe and keel with a depression between them (figs. 46-48); meso- and metatibiae sometimes medially expanded; upper side of body always with long setae and sometimes with short ones as well. 24
 - 24 Meso- and metatibiae clearly expanded medially (fig. 64 and photograph 3); body covered with setae of different length, the shorter ones relatively long and dense; inner prosternal striae slightly sinuate (fig. 46); prosternal keel almost flat longitudinally; meso-metasternal excavation shallow. *S. hispanus*
 - Meso- and metatibiae without a clear medial expansion (figs. 65 and 66); body sometimes covered by setae of different length but without dense microsetae; inner prosternal striae not sinuate (figs. 47 and 48); prosternal keel convex; meso-metasternal excavation very deep. 25
 - 25 Pronotal sides not parallel and not bisinuate (fig. 21); posterior angles of pronotum not clearly produced; pronotum regularly covered with setigerous granules; pronotum and elytra covered with setae of different length; metatibiae shorter (fig. 66) (length of metatibiae/total length body = 0.63-0.65). *S. slaoui*
 - Pronotal sides subparallel, bisinuate (fig. 20); posterior angles of pronotum clearly produced; pronotum with setigerous punctures on anterior third; pronotum and elytra with very long setae; metatibiae very long (fig. 65) (length of metatibiae/total length body = 0.73-0.75). *S. arachnoides*

***Sternocoelis viaticus* Lewis, 1892**

(Figs 1, 28 and 70)

Sternocoelis viaticus Lewis, 1892b: 263.

Sternocoelis ovalis Lewis, 1900: 252 (nov. syn.).

RE-DESCRIPTION

Colour reddish brown, shiny; body weakly convex; covered with long, aligned, yellow setae.

Frons rugose, setose; frontal stria cariniform, evanescent on epistoma; labrum weakly convex, bisinuate; mandibles robust and convex, densely punctate; antennal scape very much enlarged, rugose, bearing short setae.

Pronotum convex, subtrapezoidal (fig. 1); anterior angles obliquely truncate, slightly elevated; posterior angles slightly produced; marginal stria complete; depression opposite to base first dorsal stria; surface with setigerous punctures, larger and denser on sides and base, mixed with other non setigerous punctures. Elytra weakly convex, with large setigerous punctures and punctulate; two first dorsal striae complete, third reaching to anterior half; striae with rows of long setae; outer

subhumeral stria complete; marginal stria reaching the outer subhumeral stria on distal 2/3; epipleurae rugose, with an irregular stria.

Propygidium with coarse and dense setigerous punctures. Pygidium with smaller and sparser setigerous punctures.

Prosternal lobe and keel nearly at same level in lateral aspect, with shallow depression between them, rugose, with microsetae; prosternal keel wide; inner prosternal striae slightly divergent, not reaching lobe (fig. 28); outer prosternal striae well impressed. Meso-metasternal excavation shallow; mesosternum without lateral foveae, only with oblique elongate impressions. Metasternum with disc furnished with sparse microscopic punctures; sides fossulate; both outer lateral striae very oblique, approaching, inner one indistinct.

First abdominal sternite finely punctulate.

Legs expanded, with short setae; meso- and metatibiae triangular.

Aedeagus as figure 70.

Length 1.5 mm. Width 1.3 mm.

Type material

Two specimens of the type series of *Sternocoelis viaticus* Lewis [in NHML] have been studied. The lectotype and one paralectotype are now designated. LECTOTYPE labelled: */Sternocoelis viaticus* Lewis Type/, /Teniet Had 1.5.92/, /Type/, /G. Lewis Coll. B.M. 1926-369/. Paralectotype labelled: */Sternocoelis viaticus* Lewis Co-Type/, /Meskoutin G. Lewis 22.4.92/, /Co-Type/ and with the same last label.

The holotype of *Sternocoelis ovalis* Lewis has been examined, labelled as follows: */Sternocoelis ovalis* Lewis Type/, /Yakouren/, /Type/, /G. Lewis Coll. B.M. 1926-369/ [in NHML].

Other material examined

One specimen of the MHNG labelled as follows: /Algérie: Gde Kabylie, Azazga-Yakouren 600 m 14.V.1988 Besuchet Löbl Burkh./, */Sternocoelis* sp. 3 det. S. Mazur/.

Thirteen specimens of the MNHN (accompanied by ants) with the following labels: (1) /A. Théry 1907 L'Edough/, /not *viaticus* ?*punctulatus* Lucas/, /Muséum Paris ex Coll. P. de Peyerimhoff/, (2 and 3) /Mt. Edough Juin 1900 Dr. A. Chobaut/, */Sternocoelis viaticus*/, /Coll. Dr. V. Auzat c.v./, */Sternocoelis viaticus* Lewis/; (4) /Edough 5-94/, */S. viaticus*/; (5 and 6) /Mahoumar 1400 m L. Clouet des Pesrouches à Medjez-Amar Algérie/; (7, 8, 9 and 10) /Bugeaud L. Clouet des Pesrouches à Medjez-Amar Algérie/; (11) /A. Théry 30-1900 Edough/, /not *viaticus* ?*punctulatus* Lucas/; (12) /Région du Mont Ouarsenis, de Vauloger/; (13) /Sgag Aurés 1750 m 11 avril 1918/.

One specimen of the MNHU (accompanied by an ant): /Edough 5-94/, /Comp. par l'auteur au Type/, */Sternocoelis viaticus* Lewis/, /Zool. Mus. Berlin/.

Two specimens of the NHML labelled: (1) /Blida 10.5.94/, /G. Lewis Coll. B.M. 1926-369/; (2) /Province d'Oran Loc. ?/ and the same last label (this specimen was in the type series of *Sternocoelis pectoralis*).

One specimen in the TY: /Yakouren Chobaut/, */viaticus*/.

Distribution

This species is known from the north of Algeria.

Ecology

The species is active in spring and occurs in mountainous areas. It inhabits the nests of *Aphaenogaster gibbosa* ssp. *mauritanica* Emery.

***Sternocoelis marseulii* (Brisout de Barneville, 1866)** (Figs 2, 29, 54, 71 and 84)

Haeterius marseulii Brisout de Barneville, 1866: 367.

Sternocoelis marseulii (Brisout de Barneville): Lewis, 1888a: 153.

Sternocoelis durforti Español, 1970: 93-95 (synonymized by Yélamos, 1993: 152).

RE-DESCRIPTION

Color reddish brown, shiny; body weakly convex, broadly oval; covered with long yellow setae.

Frons with setigerous pores; frontal stria cariniform, irregular, longitudinally crossing epistoma; labrum with medial depression, bisinuate in front; mandibles large, convex; antennal scape very enlarged, with short setae.

Pronotum trapezoidal (fig. 2), with fine and sparse setigerous pores and long yellow setae; anterior angles weakly produced, rounded; posterior angles slightly produced; base of prosternum with shallow impression opposite to base first dorsal stria; marginal stria complete. Elytra moderately convex; doubly punctate, punctures irregular and sparse, with long erect setae along striae; first dorsal stria complete, second reduced apically and third interrupted at middle; outer subhumeral stria joined to marginal stria at middle; epipleurae smooth, bistriate, joined together and also with marginal stria.

Propygidium convex, with dense setigerous pores and setae. Pygidium convex, finely punctulate.

Prosternum with keel at higher level than lobe (fig. 29); lobe very rugose, not prominent; inner prosternal striae strong, joined in front, interspace coarsely and densely punctate; sides keel very rugose; outer striae obsolete. Meso-metasternal excavation shallow; mesosternum without lateral foveae, but with fine oblique impressions. Metasternum finely punctulate on disc; without inner lateral stria, medial stria strong, very arcuate, reaching metacoxae, and outer stria fine and short; sides fossulate.

First abdominal sternite convex, finely punctulate on disc, with coarse punctures on sides.

Legs short, expanded (fig. 54); meso- and metatibiae triangular, punctate and setose.

Aedeagus as figure 71 and spiculum gastrale as figure 84.

Length 1.3-1.4 mm. Width 1.1-1.2 mm.

Type material

Seven specimens of the type series of *Haeterius marseulii* Brisout de Barneville have been examined. The lectotype and five paralectotypes are now designated. LECTOTYPE [in MNHN] labelled: /Type/, /*Marseulii* Ch. Bris./, PARALECTOTYPES, three specimens of the same Museum and with identical labels. One specimen of the MNHN labelled: /Escorial (Espagne)/, /Type/, /*Marseulii* Bris., Coll. Théry, S. Théry/. The other two specimens of the MNHU are labelled as follows: (1) /Type/, /*Marseulli*, Bris. typ. Escorial/, /coll. J. Schmidt/, /*Marseulii* Bris./, /Zool. Mus. Berlin/; (2) /Escorial, Brisout/, /Type/, /Zool. Mus. Berlin/, /*Marseulii*/.

The holotype and six paratypes of *Sternocoelis durforti* Español have been studied [holotype and five paratypes in MZ and one paratype in MNHN]. Holotype, labelled: /Pla dels Motllats, Montral 25-V-69, F. Español leg./, /*Sternocoelis durforti* n. sp., F. Español det./,

/Tipo/. Paratypes, three specimens with same labels as the holotype, except the paratype label. One specimen labelled: /Farena, 24-V-69, F. Español leg./, /*Sternocoelis durforti* n. sp., F. Español det./, /Paratipo/. One specimen with the same second and third labels, as well as the first one /Pinetell, 22-VI-69, F. Español leg./. One specimen [in MNHN] labelled /Farena, Prades, 22-VI-69, F. Español leg./, /Nido *Aphaenogaster*, F. Español leg./, /Paratypus/, /*Sternocoelis durforti*, F. Español det./.

Other material examined

One specimen of the DEI: /*Hetaerius Marseuli* Bris., S. Cordoba, Ehlers/, /Coll. L.v. Heyden, DEI Eberswalde/.

Two specimens of the MNCN: /Escorial, 20.V.1926/, /*Sternocoelis marseulii*/.

Five specimens of the MNHN (1) /Escorial, Lewis apr. 98/, /Coll. Bonnaire/, /*Marseuli* Brisout/, /Coll. Dr. V. Auzat/, /*Sternocoelis Marseuli*, Brisout/; (2) /Huescar, 20.5.900/, /Espagne, ex. Escalera/, /comparé au Type, 18.VI.1923, Dr. Auzat/, /Coll. Dr. V. Auzat/, /*Sternocoelis marseuli*, Brisout/; (3) /Escorial, 30-V-1926, Escalera/, /Coll. Dr. V. Auzat/, /*Sternocoelis marseuli*, Brisout/; (4 and 5) /Escorial, 14-V-1926, Escalera/, /Coll. Dr. V. Auzat/, /*Sternocoelis marseuli*, Brisout/.

Eleven specimens of the MZ. Two specimens /Pla dels Motllats, Mont-ràl, 25-V-69, F. Español leg./. Four specimens /Farena, Serra de Prades, 24-V-69, F. Español leg./. Two specimens /El Pinetell, Serra de Prades, 22-VI-69, F. Español leg./. Three specimens /El Pinetell, Serra de Prades, 31-V-71, F. Español leg./. One specimen /Plana d'Ancosa, La Llacuna, 1.VIII.71, *Aphaenogaster* sp./.

One specimen in TY labelled: /El Pinetell, 13.6.82, F. Español leg./.

Distribution

This species mainly occurs in the mountains of central and north-eastern Spain (Sierra del Guadarrama, Serra de Prades and Serra de la Mussara). It is also known from a few localities from the south of Spain (Sierra de Córdoba and Huéscar, Granada).

Ecology

This species is active mainly in May and June in mountainous areas. They inhabit nests of several species of *Aphaenogaster*.

Sternocoelis vaucheri Lewis, 1896

(Figs 51 and 72)

Sternocoelis vaucheri Lewis, 1896: 62.

RE-DESCRIPTION

Colour light brown, shiny; body strongly convex; covered with long yellow setae.

Frons rugose, with short setae; frontal stria cariniform, evanescent on epistoma; labrum flat und truncate; mandibles large, convex, punctulate; antennal scape strongly enlarged, rugose.

Pronotum subtrapezoidal, convex; anterior angles rounded, weakly produced; posterior angles produced; marginal stria fine, complete; surface uniformly impressed with setigerous punctures, coarser and denser on sides, and apical half with long

setae; small basal depression opposite to base second dorsal stria. Elytra very wide and convex, with mixture of fine, dense punctures, and several setigerous punctures; first dorsal stria complete, second and third reaching middle of elytra; inner subhumeral stria complete, and marginal one joined medially with outer subhumeral stria; epipleurae with a well impressed, irregular, and abbreviated stria.

Propygidium with coarse and dense punctures. Pygidium sparsely punctate.

Prosternum with keel at a more prominent level than lobe; lobe very reduced; inner prosternal striae well impressed, joined in front; prosternal keel flat, sparsely punctate; prosternal keel sides and lobe rugose; outer prosternal stria very faint. Meso-metasternal stria shallow; mesosternum without deep foveae, only with an oblique elongate impression. Disc of metasternum smooth and convex; inner lateral stria fine, not reaching middle, medial strong, complete and oblique, the outer stria obsolete (fig. 51).

First abdominal sternite convex and smooth.

Legs short, with meso- and metatibiae weakly expanded, punctate and setose.

Aedeagus as figure 72.

Length 1.3-1.4 mm. Width 1.0-1.1 mm.

Type material

Two specimens of the type series have been studied [both in the NHML]. The lectotype and one paralectotype are now designated. LECTOTYPE ♂ labelled: */Sternocoelis vaucheri* Lewis, *Type*, /2.96, Tangier/, */Type*/, /G. Lewis Coll., B.M. 1926-369/. PARALECTOTYPE ♂ labelled: */Tanger 1896, Vaucher*/, /much more convex than *Marseuli* Bris./, /G. Lewis Coll., B.M. 1926-369/ (accompanied by an ant).

Other material examined

There are two specimens in MNHN labelled as follows: (1) */Tanger*/, */Vaucheri*, Lewis, *Tanger*/. (2) */1897, Tanger*/, */Maroc, ex Musaeo, H. Vaucher, 1908*/, */Sternocoelis Vaucheri* Lew./.

Distribution

This species is known from Tangier (north of Morocco).

Ecology

The beetle is apparently active only in January and February at low elevations. It occurs in the nests of *Aphaenogaster sardoa* Mayr, *A. strioloides* Forel and *A. crocea* André.

Sternocoelis lewisi (Reitter, 1883)

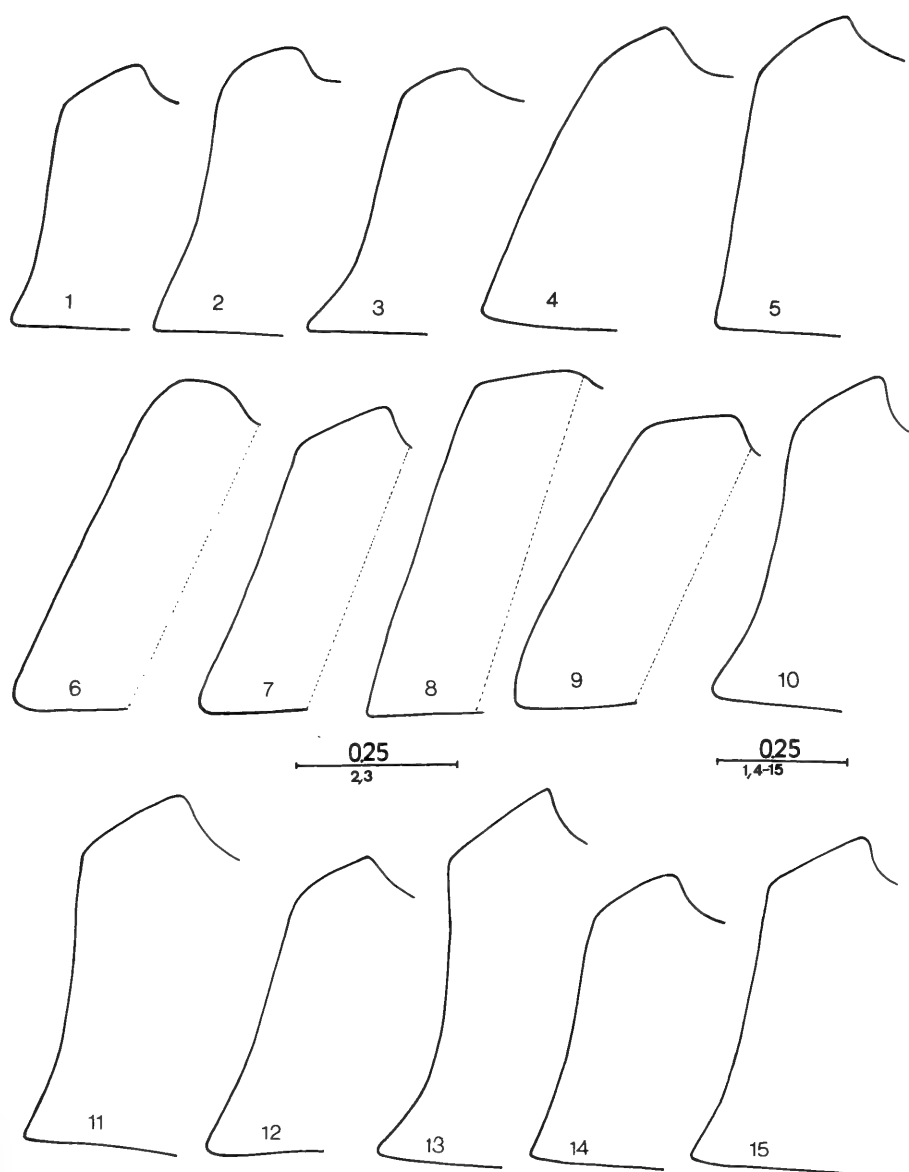
(Figs 3 and 30)

Hetaerius lewisi Reitter, 1883: 143.

Sternocoelis lewisi (Reitter): Lewis, 1888a: 150.

RE-DESCRIPTION

Colour dark brown, shiny; body strongly convex; surface covered with mid-length yellow setae.



FIGS 1-15

Left margin of pronotum: *Sternocoelis viaticus* Lewis (1); *S. marseulii* (Brisout de Barneville) (2); *S. lewisi* (Reitter) (3); *S. puberulus* (Motschulsky) (4); *S. merklüi* (Schmidt) (5); *S. otini* Peyerimhoff (6); *S. marginalis* Normand (7); *S. grandis* (Reitter) (8); *S. robustus* (Pic) (9); *S. fuscus* (Schmidt) (10); *S. incisus* (Schmidt) (11); *S. alluaudi* Théry (12); *S. acutangulus* (Lewis) (13); *S. pluristriatus* (Fairmaire) (14); *S. bedeli* (Lewis) (15). Scale in mm.

Frons rugose, with dense setigerous pores; frontal stria cariniform, regular, evanescent on epistoma; labrum large, weakly depressed and bisinuate; mandibles large, convex, with short setae; antennal scape very enlarged, setose.

Pronotum subtrapezoidal, gradually enlarged posteriorly (fig. 3); anterior angles slightly produced, neither elevated nor truncate; surface covered with dense and coarse punctures; with a deep depression near to base first dorsal stria; marginal stria complete. Elytra strongly convex, humeral angles rather enlarged, covered with dense, deep punctures; marginal stria joined with outer subhumeral stria at apical 2/3 of elytra; first dorsal stria complete, second stria exceeding 2/3 elytral length and third reaching middle; epipleurae rugose, without striae.

Propygidium and pygidium sparsely punctate.

Prosternal lobe rugose, not prominent, at a lower level than keel (fig. 30); prosternal keel with distinct outer striae; inner prosternal striae well impressed and parallel; keel narrowed in front, rugose, without striae. Meso-metasternal excavation very deep; mesosternum without lateral foveae. Metasternum finely and densely punctate on disc; inner lateral stria reaching middle or 2/3; other two striae more lateral, not reaching metacoxae; sides with coarse and irregular punctures.

First abdominal sternite finely and densely punctate.

Legs of normal length, meso- and metatibiae very expanded triangular and setose.

Male not known.

Length 1.8-2.1 mm. Width 1.6-1.8 mm.

Type material

Two specimens of the type series have been examined. The lectotype and one paralectotype are now designated [both in MNHU]. LECTOTYPE ♀ labelled: */Hetaerius Lewisi* m.n. sp./, */Morea Cumani Brenske/*, */Zool. Mus. Berlin/*. PARALECTOTYPE ♀ labelled: */Type/*, */Lewisi* Rtt. typ./, */Morea Hagios Wlassis Brenske/*, */coll. J. Schmidt/*, */Zool. Mus. Berlin/*, */Lewisi* Reitt./.

Other material examined

Two specimens of the MNHU with the labels: */Missolunghi/*, */Zool. Mus. Berlin/*.

Distribution

This species is known from several localities in Greece.

Ecology

No biological data are available for this species.

Sternocoelis diversepunctatus Pic, 1911

(Fig. 31)

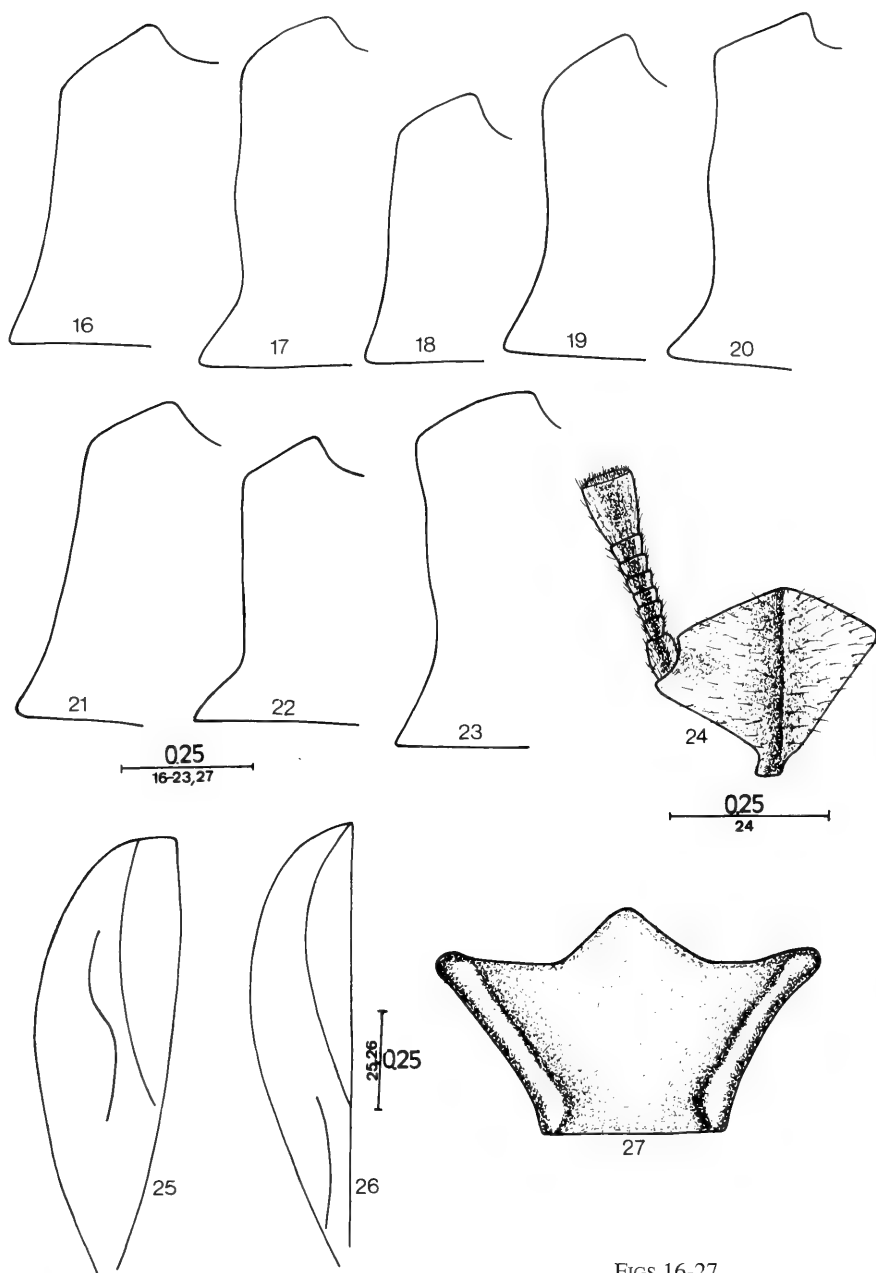
Sternoscaelis diversepunctatus Pic, 1911: 137 (error).

Sternocoelis diversepunctatus Pic: Bickhardt, 1917: 157.

Sternocoelis diversipunctatus Pic: Menozzi, 1942: 7 (error).

RE-DESCRIPTION

Colour reddish brown, shiny; body weakly convex, oval; body covered with short yellow setae.



FIGS 16-27

Left margin of pronotum: *Sternocoelis punctulatus* (Lucas) (16); *S. atlantis* Théry (17); *S. setulosus* (Reitter) (18); *S. hispanus* (Rosenhauer) (19); *S. arachnoides* (Fairmaire) (20); *S. slaoui* Théry (21); *S. comosellus* (Fairmaire) (22); *S. espadaleri* n. sp. (23). Left antenna in ventral view of *S. alluaudi* Théry (24). Left epipleura: *S. puberulus* (Motschulsky) (25); *S. robustus* (Pic) (26). Disc of mesosternum of *S. arachnoides* (Fairmaire) (27). Scale in mm.

Frons with dense setigerous punctures; frontal stria cariniform; labrum bisinuate; mandibles large, convex, finely punctulate; antennal scape very enlarged, rugose and setose.

Pronotum subtrapezoidal; disc convex; anterior angles truncate, weakly produced; posterior angles slightly produced; marginal stria complete; surface coarsely and densely punctate, mainly laterad, punctures are setigerous variety; setae also present laterad; base pronotum with deep depression. Elytra weakly convex; first dorsal stria well impressed and complete, second not reaching apex and third only reaching middle; marginal stria joined with outer subhumeral stria apically; surface with dense and well impressed punctures, sides with several setigerous punctures and setae; epipleurae rugose, with irregular medial part of stria.

Propygidium and pygidium convex, with rather dense well impressed punctures.

Prosternal lobe rugose, at lower level than keel and clearly bisinuate (fig. 31); prosternal keel rugose and narrow; inner prosternal striae obsolete, not parallel and approaching, with short medial remnants of outer striae. Mesosternum finely punctate; meso-metasternal depression not deep; meso-metasternum with well impressed punctures and without lateral foveae. Metasternum with fine inner lateral stria, only on anterior third; medial stria almost reaching metacoxae; outer stria shorter; sides fossulate.

First abdominal sternite finely and densely punctate.

Legs very expanded and setose; meso- and metatibiae triangular.

Male not known.

Length 2.0 mm. Width 1.9 mm.

Type material

It has been possible only to examine the holotype ♀ deposited in the Pic's collection deposited in the MNHN with the label /Type *Sternocoelis diversepunctatus* Pic/ (accompanied with two ants).

Distribution

Described from Cyprus and subsequently recorded from Rodi Island (Aegean Sea, Italy) (MENOZZI, 1942).

Ecology

This species was observed in April in nests of *Aphaenogaster balcanica* Emery.

Sternocoelis puberulus (Motschulsky, 1858)

(Figs 4, 25, 32 and 73)

Hetaerius puberulus Motschulsky, 1858: 188.

Eretmotes palumboi Ragusa, 1882: 7 (synonymized by Lewis, 1888a: 150).

Sternocoelis puberulus (Motschulsky): Lewis, 1888a: 150.

RE-DESCRIPTION

Colour reddish brown, shiny; body form very convex, oval; surface covered with long yellow setae.

Frons coarsely and densely punctate; frontal stria cariniform, regular, evanescent on epistoma; labrum slightly depressed and bisinuate; mandibles large, convex, with short setae; antennal scape very enlarged, setose.

Pronotum subtrapezoidal, convex, very enlarged posteriorly (fig. 4); anterior angles slightly elevated, not truncate; posterior angles weakly produced; marginal stria interrupted apically; surface with mixture of large, irregular, dense setigerous pores, and same smaller punctures; pronotum base with deep depression opposite to base of second dorsal stria. Elytra convex, very enlarged, with well impressed, dense punctures, without setigerous pores; marginal stria very strong but short, joined with outer subhumeral stria at middle, complete; first dorsal stria complete, second surpassing middle, less impressed, third dorsal stria finely impressed, as a short basal trait; epipleurae rugose, with short irregular stria (fig. 25).

Propygidium and pygidium with coarse, regular and dense punctures, without setigerous pores.

Prosternal lobe emarginate, at a lower level than keel (fig. 32); outer prosternal stria indistinct by rugosity of keel and lobe; inner prosternal striae parallel, only distinct up to middle, with a depressed and densely punctate area between them. Meso-metasternal excavation shallow; mesosternum without lateral foveae near to mesocoxae; inner metasternal lateral stria only reaching middle, medial one cariniform and reaching metacoxae, and outer stria very short, approaching the medial stria; sides of metasternum with short setae and with coarse irregular, dense punctures.

First abdominal sternite finely punctate.

Legs setose, rather expanded, meso- and metatibiae triangular.

Aedeagus as figure 73.

Length: 1.5-1.8 mm. Width 1.4-1.7 mm.

Type material

The holotype of *Hetaerius puberulus* has been studied, labelled as follows: /*Sicilia*/, /*Haeterius puberulus* Motsch. *Sicilia*/, deposited in ZMMLSU.

Two specimens have been studied apparently from the type series of *Eretmotus palumboi* Ragusa. A holotype has not been designated. They are not designated here as lectotype and paralectotype because I doubt that they really belong to the type material.

Other material examined

Four specimens have been studied of the DEI and labelled as follows: (1) /*Sicilia*/, /Coll. Kraatz/, /Bickhardt det./, /*Hetaerius puberulus*/; (2) /*Sicilia* 1906 Ficuzza O. Leonhard/, /*Sternocoelis puberulus* Motsch. A. Reichardt det./; (3) /*Sicil*/, /Coll. Stierlin/, /*H. puberulus* Motsch./; (4) /*Eretmotes Palumboi* Rag. *Sicil*. Ragusa 15 fres./, /Coll. L.v. Heyden DEI Eberswalde/.

Three specimens of the MNHN labelled as follows: (1) /*cavisternus*/, /136/, /Muséum Paris coll. de Marseul 1980/; (2) /*Sicilien* Ragusa/, /Muséum Paris 1933 Coll. Desbordes/, /*puberulus* Coll. Bickhardt/; (3) /*Sicilia*/, /Coll. Bonnaire/, /*Hetaerius puberulus* Motsch. Er. *Palumboi* Rag./, /Coll. Dr. V. Auzat/, /*Sternocoelis puberulus* Mots./.

Four specimens of the MNHU, two were labelled /*Sicile* Baudi/, /Coll. J. Schmidt/, /Zool. Mus. Berlin/, /*puberulus* Motsch./, One specimen /*Sicilia* Ficuzza 84 E. Ragusa/, /Zool. Mus. Berlin/. One specimen labelled /*Eretmotes Palumboi* Ragusa typ. *Sicilien*/, /Zool. Mus. Berlin/.

Two specimens of the ZM, both labelled /Messina Schiöde/.

Two specimens of the TM labelled: (1) /Sicilia/, /*puberulus* Sicilia Baudi/, /*Sternoc. puberulus* Motsch. Coll. Reitter/; (2) /Sicilia Ragusa/, /Coll. Reitter/, /Paratypus *Eretmotes Palumboi* Ragusa/.

Distribution

This species is known from several localities in Sicily, and also recorded from Corsica and Sardinia (VIENNA, 1980).

Ecology

It inhabits mountainous areas, and is active in spring. It has been recorded from nests of *Formica fusca* Linnaeus.

Sternocoelis merklia (Schmidt, 1885)

(Figs 5, 33, 52 and 74)

Hetaerius merklia Schmidt, 1885a: 238.

Sternocoelis merklia (Schmidt): Lewis, 1888a: 154.

RE-DESCRIPTION

Colour reddish brown, shiny; body very convex, oval; with few, yellow, mid-length setae only (in some specimens setae are more dense).

Frons slightly rugose and with setigerous punctures; frontal stria cariniform, evanescent on epistoma; labrum weakly depressed, bisinuate; mandibles large, convex, without setae; antennal scape punctate, very enlarged, with short setae.

Pronotum with anterior angles produced (fig. 5), somewhat elevated; posterior angles not produced; sides not parallel; pronotal surface with dense setigerous punctures, larger on sides and base, smaller apically; disc smooth, longitudinally convex; marginal stria complete; small basal depression opposite first dorsal stria. Elytra sparsely and finely punctate; medial sutural zone very convex longitudinally, like pronotum; marginal stria joining outer subhumeral stria on 2/3; first, second and third dorsal striae complete, fourth as a short trait, arcuate toward suture, sometimes obsolete; epipleurae rugose, with a short irregular stria.

Propygidium and pygidium coarsely and densely punctate, setose.

Prosternal lobe rugose and bisinuate; prosternal lobe and keel at a same level (fig. 33); lobe not prominent; keel rugose; inner prosternal striae parallel up to 2/3 elytral length, thence converging at apical end; outer prosternal striae well impressed. Meso-metasternal excavation shallow; mesosternum without lateral foveae. Metasternal disc finely and densely punctate; sides fossulate; both inner striae reaching metacoxae, outer striae shorter (fig. 52).

First abdominal sternite finely and sparsely punctate.

Legs of normal length, with short setae; meso- and metatibiae triangular.

Aedeagus as in figure 74.

Length 1.8-2.0 mm. Width 1.6-1.8 mm.

Type material

The holotype (♀) has been studied [in MNHU]: /Type/, /*Merklii* Schmidt, typ. Constantinop./, /Turkei Constantinopol M./, /Coll. J. Schmidt/, /Zool. Mus. Berlin/, /*Merklii* Schmidt/.

Other material examined

One specimen of the DEI (accompanied by an ant) labelled /Bulgar Rumel Backovo 11.V.09 Rambousek/, /*Messor barbarus stuctor* Latr. var. *mistica* Nyl./, /*Hetaerius merkli* det. J. Müller/, /coll. Leonhard/.

One specimen of the MHNG, with the first label like the former, moreover /*Sternocoelis Merkli* Schmidt H. Desbordes det. 22/.

Three specimens of the MNHN, two specimens also with the same first label, moreover /Coll. Dr. V. Auzat/. One specimen labelled: /Paxos S. Corfu: (Kerkira): 2 km NW Galos 17.4.81 Scheuern leg./, /Muséum Paris Coll. J. Théron d./, /Olivenhain/.

One specimen of the NHMW labelled: /*Lewisii* Reitt. Bittner Graecia/, /Isthmus/.

Distribution

This species is only known from a few localities in Greece (Kerkira, Corfu), Bulgaria (Rumel, Backovo) and Turkey (Istanbul).

Ecology

It occurs at lower altitudes and is active in spring. It inhabits the nests of *Messor structor* (Latreille).

Sternocoelis otini Peyerimhoff, 1949

(Figs 6, 34 and 57)

Sternocoelis otini Peyerimhoff, 1949: 264.

RE-DESCRIPTION

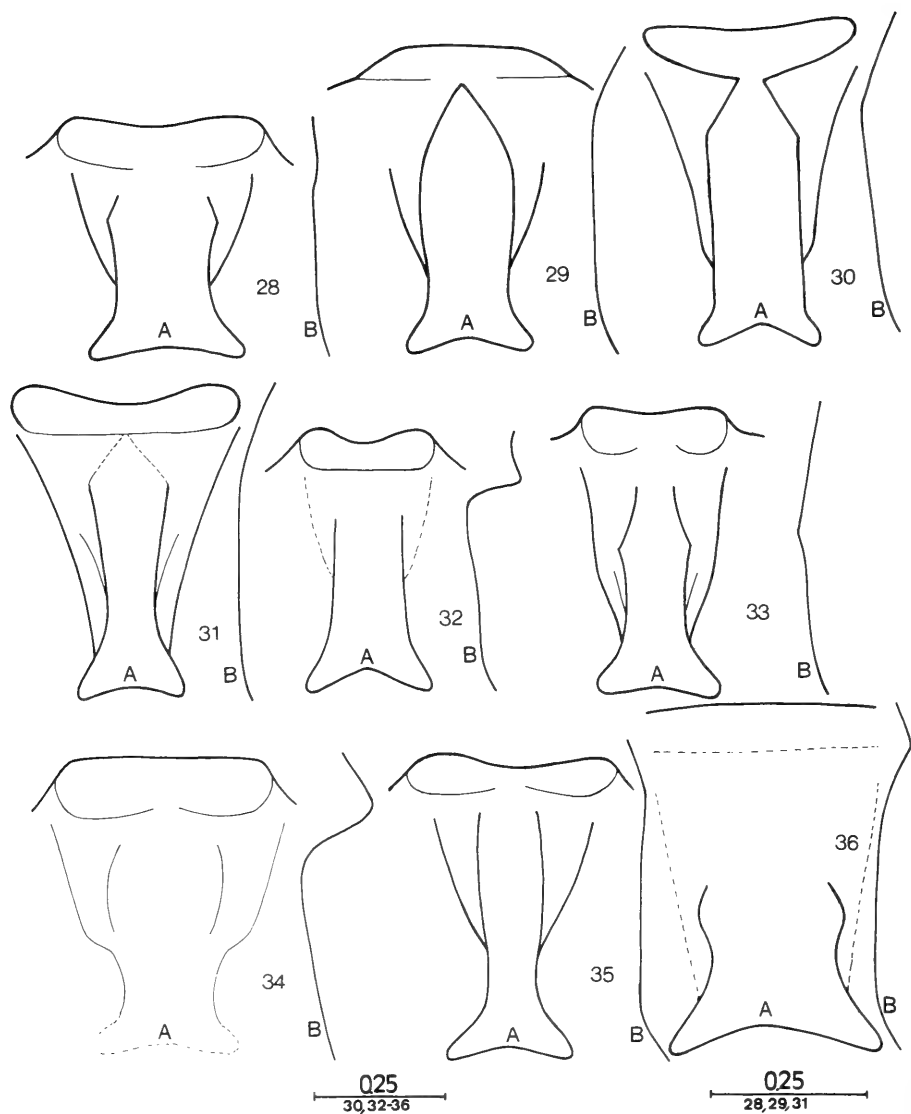
Colour reddish brown, shiny; body form weakly convex, oval; surface covered with short yellow setae.

Frons finely punctulate; frontal stria cariniform, faint; labrum slightly depressed; mandibles large and convex; antennal scape very enlarged, finely rugose and setose.

Pronotum subtrapezoidal, rather convex with sides clearly separated, explanate (fig. 6); anterior angles neither produced nor elevated; posterior angles not produced; marginal stria very fine or obsolete; surface sparsely punctate; base of pronotum with a clear depression. Elytra weakly convex, wide, finely punctulate; first dorsal stria complete, second and third reaching middle; marginal stria joined to outer subhumeral; epipleurae slightly rugose, without striae.

Propygidium and pygidium with setigerous pores and fine short setae.

Prosternal lobe prominent, at lower level than keel and separated by a depression (fig. 34); prosternal keel wide, very rugose, with only a medial short part of inner prosternal stria; outer prosternal stria distinct. Meso-metasternal excavation very deep, mesosternum in a right angle with keel in lateral view, without lateral foveae. Metasternum finely punctulate; inner stria reaching metacoxae, other two striae long and oblique; sides fossulate.



FIGS 28-36

Prosternal lobe and keel, ventral view (A), outline (B): *Sternocaelis viaticus* Lewis (28); *S. marseulii* (Brisout de Barneville) (29); *S. lewisi* (Reitter) (30); *S. diversepunctatus* Pic (31); *S. puberulus* (Motschulsky) (32); *S. merklui* (Schmidt) (33); *S. otini* Peyerimhoff (34); *S. marginalis* Normand (35); *S. laevidorsis* (Fairmaire) (36). Scale in mm.

First abdominal sternite finely punctulate.

Legs long and slender; tibiae regularly expanded on apical half (fig. 57), not triangular

Male unavailable.

Length 2.4 mm. Width 2.2 mm.

Type material

Although the original description was based on two specimens presently only a single specimen remains. The only examined specimen (accompanied by an ant) has been designated LECTOTYPE, and is labelled: ♀ /Dayet Ifrah, 27-6-43, Otin/, /*Sternocoelis otini* Type/, /*Cataglyphis viatica* subs. *mauritanica* Emery/, /Moyen Atlas, alt. 1600 m/, [in MNHN].

Distribution

This species is only known from the type locality near Ifrane (Moyen-Atlas, Morocco).

Ecology

This species occurs in a mountainous area. It has been collected at the end of June in a nest of *Cataglyphis mauritanicus* Emery.

***Sternocoelis marginalis* Normand, 1915**

(Figs 7, 35 and 58)

Sternocoelis marginalis Normand, 1915: 255.

RE-DESCRIPTION

Colour light brown, shiny; body weakly convex; surface with dense setae of two different lengths on dorsal surface, glabrous on ventral surface.

Frons sparsely punctate; frontal stria cariniform, evanescent on epistoma; labrum slightly depressed, bisinuate; mandibles large and convex, smooth; antennal scape very enlarged, sparsely punctate and setose.

Pronotum subtrapezoidal (fig. 7); disc convex, with sides explanate; deep basal depression opposite to second dorsal stria; anterior angles not elevated and posterior angles not produced; marginal stria complete; with scarce and small setigerous granules. Elytra rounded, weakly convex, only with small setigerous granules; first dorsal stria complete, second and third confined to anterior half; marginal and outer subhumeral striae joined; epipleurae smooth, with an irregular anterior stria and another apical.

Pygidium with short setae, scantier on pygidium.

Prosternal lobe and keel separated by a shallow depression; prosternal lobe weakly prominent, not emarginate (fig. 35); prosternal keel narrow, with distinct inner striae, cariniform, complete, subparallel, distant at base; finely punctate between striae; outer prosternal striae obsolete. Mesosternum without lateral foveae; meso-metasternal excavation very deep. Metasternal disc smooth; sides regularly punctate; inner stria reaching metacoxae, the other two striae very oblique and long.

First abdominal sternite smooth.

Legs long and slender, regularly expanded in apical half (fig. 58), with short setae.

Aedeagus similar to *S. laevidorsis*.

Length 2.0-2.2 mm. Width 1.8-1.9 mm.

Type material

Four specimens of the type series have been studied. The lectotype and three paralectotypes are designated here [all in MNHN]. LECTOTYPE (accompanied by an ant) labelled: /T. Le Kef, Dr. Normand/, /*Marginalis* Norm./, /Paratype/. PARALECTOTYPES: two specimens with the two first labels as in the lectotype, and additional labels: /Coll. Dr. V. Auzat/ and /*Sternocoelis marginalis* Norm./ (accompanied by ants). One specimen labelled: /Tunis Le Kef/, /*Sternocoelis marginalis* Norm./.

Distribution

Only known from the environs of Le Kef (Tunisia).

Ecology

The type material was collected in the spring in the nests of *Cataglyphis mauritanicus* Emery in a mountainous area.

Sternocoelis laevidorsis (Fairmaire, 1876)

(Figs 36 and 75)

Hetaerius laevidorsis Fairmaire, 1876: 37.

Sternocoelis laevidorsis (Fairmaire): Lewis, 1888a: 155.

Sternocoelis laevidorsis var. *major* Pic, 1905: 129.

Sternocoelis laevidorsis var. *semiopacus* Normand, 1915: 256.

RE-DESCRIPTION

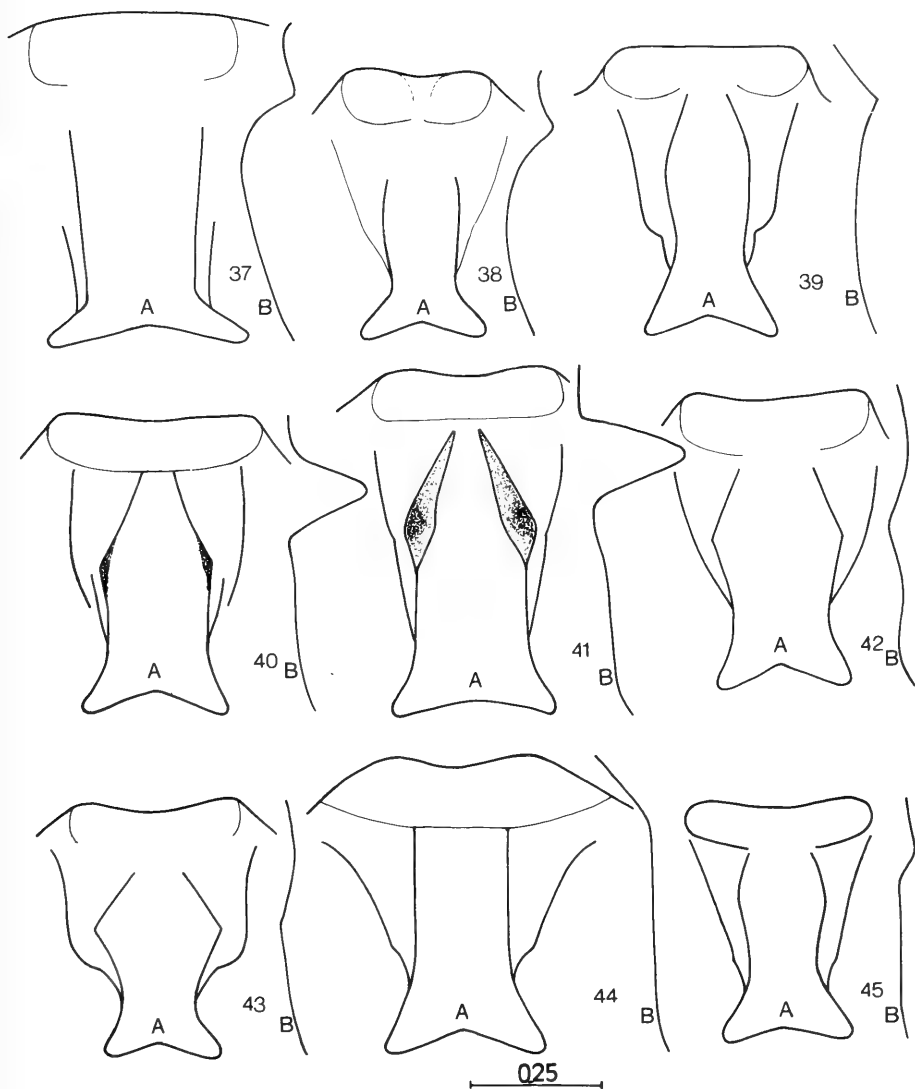
Colour reddish brown; body weakly convex, oval; dorsal surface with sparse and short setae laterally.

Frons wide, finely and sparsely punctate; frontal stria cariniform, evanescent on epistoma; labrum slightly depressed; mandibles large, convex and finely punctulate; antennal scape very enlarged, punctate, with short setae.

Pronotum finely punctulate, scanty on disc, rugose and denser on sides; sides of pronotum well separated from disc, explanate; marginal stria complete; anterior angles truncate, not elevated; posterior angles not produced. Elytra weakly convex, finely punctulate, with dense alutaceous microsculpture, producing a dull texture; first dorsal stria complete; second stria very fine, somewhat surpassing middle; third stria as a short and fine anterior trait; marginal stria coming joining outer subhumeral; epipleurae sparsely punctate, with an irregular segment of stria.

Propygidium and pygidium convex, well impressed and densely punctate.

Prosternal keel and lobe very rugose; lobe not bisinuate, at a lower level than keel (fig. 36); keel wide; inner prosternal striae faint, only on basal half; outer striae obsolete. Mesosternum smooth, without lateral foveae; meso-metasternal excavation



FIGS 37-45

Prosternal lobe and keel, ventral view (A), outline (B): *Sternocoelis grandis* (Reitter) (37); *S. robustus* (Pic) (38); *S. fuscus* (Schmidt) (39); *S. incisus* (Schmidt) (40); *S. acutangulus* (Lewis) (41); *S. bedeli* (Lewis) (42); *S. punctulatus* (Lucas) (43); *S. atlantis* Théry (44); *S. setulosus* (Reitter) (45). Scale in mm.

deep. Metasternum finely punctulate, with three long striae, inner stria reaching metacoxae; sides fossulate.

First abdominal sternite finely and evenly punctulate.

Legs relatively long and slightly expanded.

Aedeagus as figure 75.

Length 2.2-2.5 mm. Width 2.1-2.2 mm.

Type material

The type material of *Hetaerius laevidorsis* Fairmaire has not been located.

Two specimens of the type series of *S. laevidorsis* var. *major* Pic have been studied. The lectotype and one paralectotype are now designated [all in MNHN]. LECTOTYPE (accompanied by an ant) labelled: /Kerratra, 8.1901, de Vauloger/, /Type/, /major Pic (Alg.)/. PARALECTOTYPE, one specimen labelled as the lectotype.

Two specimens of the type series of *S. laevidorsis* var. *semiopacus* Normand have been studied. The lectotype and one paralectotype are now designated [all in MNHN]. LECTOTYPE (accompanied by an ant) labelled: /T. Sousse, Dr. Normand/, /laevidorsis var. semiopacus Frm. Co-Type/. PARALECTOTYPE, one specimen and one ant having the same first label, and an additional label: /v. semiopacus Norm./, /Coll. Dr. V. Auzat/, /S. laevidorsis v. semiopacus Norm./.

Other material examined

One specimen of the DEI labelled: /*Sternocoelis laevidorsis* Fairm./, /Kairouan Tunis Dr. Santsobil/, /Catagl. bicolor/, /Reichensperger determ./.

One specimen of the MHNG labelled as follows: /Teniet el Had/, /grandis Reitt./.

Eight specimens of the MNHN labelled: (1) /Kerratra, Algérie, Coll. Théry/, /*Sternocoelis laevidorsis* Frm./; (2) /Sgaeg Aurés, 20 juin 1922/, (3) /T. Sousse, Dr. Normand/, (4) /*Sternocoelis laevidorsis* Fairm./, /Kairouan, Tunis, Dr. Santsobil/, /Coll. Reichensperger/, /laevidorsis Frm./; (5) /Bled Thalà (Oued Edehelie) 25.1.1901/, /*Sternoscelis laevidorsis* Fair./; (6) /Yakouren (Algérie) Juin 1902 Dr. A. Chobaut/, /Coll. Dr. V. Auzat/, /*Sternoscelis laevidorsis* Fair./; (7) /Bir Becha, Reg. de Gafra, 20.1.1901/, /*Sternocoelis laevidorsis* Fair./; (8) /Tunisie, Sbi Kha Fr. F. Santsobil/, /12.1.01/, /*Sternoscelis laevidorsis* Fairm./, /Hadjeb El Aïoun, Tunisie, 1.IV.96/, /Coll. Dr. V. Auzat/, /*Sternocoelis laevidorsis* Frm./.

One specimen of the TY labelled: /Yakouren (Kabylie) Juin 1902, Dr. A. Chobaut/, /*Sternocoelis laevidorsis* Fairm./.

Distribution

This species occurs in the north-east of Algeria and the north of Tunisia.

Ecology

It inhabits mountainous areas and is active from January to June. They have been found with the ants *Cataglyphis bicolor* (Fabricius) and *C. viatica* (Fabricius).

Sternocoelis grandis (Reitter, 1883)

(Figs 8, 37 and 59)

Hetaerius grandis Reitter, 1883: 143.

Sternocoelis grandis (Reitter): Lewis, 1888a: 151.

RE-DESCRIPTION

Colour, reddish brown, somewhat shiny; body convex, broadly oval; sides of body with short yellow setae.

Frons weakly depressed, rugosely punctate; frontal stria strongly cariniform, complete on sides, evanescent on epistoma; labrum weakly depressed; mandibles large, rugose and convex; antennal scape very enlarged, antennal surface rugose and setose.

Pronotum subtrapezoidal (fig. 8); disc weakly convex, sides clearly separated, explanate; anterior angles neither produced nor elevated; posterior angles not produced; marginal stria strong, distinct; disc coarsely and densely punctate; sides more coarsely and densely punctate, with deeper punctures, rugose next to marginal stria; pronotal base with a distinct depression. Elytra very broad and slightly convex; finely and densely punctate, mainly on anterior half, becoming rugose; first dorsal stria surpassing middle, second slightly shorter and third only marked by an elongate impression reaching middle; marginal stria strong, cariniform, complete, joined to outer subhumeral stria apically; surface between these two striae rugose, with setigerous punctures; epipleurae densely rugose, with two irregular striae, one of them almost complete, the other confined to apical half.

Propygidium and pygidium with large and dense punctures.

Prosternal lobe at lower level than keel, rugosely punctate and with shallow medial depression (fig. 37); prosternal keel densely rugose, with inner striae obsolete, subparallel, and the outer striae indistinct; sides of keel rugose. Mesosternum with dense and well impressed punctures, almost in a right angle to prosternum in lateral view, without lateral foveae; meso-metasternal excavation very deep. Metasternum with well impressed, irregular and very dense punctures on disc, deeper, larger and denser on sides; striae well impressed, weakly cariniform, the inner reaching metacoxae, the other striae reduced.

First abdominal sternite coarser and denser punctured than metasternum.

Legs setose, densely punctate; protibiae and mesotibiae expanded (fig. 59).

Male unknown.

Length 2.3 mm. Width 2.1 mm.

Material examined

One specimen ♀ [in MHNG] labelled as follows: /O. Jordanie, Haman al Sarah, 3-4-1964, J. Klapperich/, /*Sternocoelis grandis*/.

Distribution

The original description mentions "Talysch: Rasano". This is an unlikely type locality and possibly erroneous. It is possible that it lives either in Greece or in Turkey. The species is known from Jordan. Its presence here is a considerable range extension for the genus *Sternocoelis*.

Ecology

The species was collected early in spring.

Sternocoelis robustus Pic, 1910

(Figs 9, 26 and 38)

Sternoscaelis robustus Pic, 1910: 33 (*lapsus calami*).

Sternocoelis robustus Pic: Bickhardt, 1917 (justified emendation).

RE-DESCRIPTION

Colour reddish brown, shiny; body weakly convex, oval; dorsal surface of body with short setae and additional longer setae on sides and legs.

Frons finely punctate; frontal stria regular, cariniform, evanescent on epistoma; labrum slightly depressed; mandibles large, convex and densely punctate; antennal scape very enlarged and with short setae.

Pronotum covered with fine and dense punctures, somewhat rugose on sides; disc very convex, separated from sides by a well marked oblique impression; sides explanate; marginal stria complete; anterior angles truncate, not elevated, posterior angles not produced (fig. 9); deep basal depression opposite to second dorsal stria.

Elytra weakly convex, finely and densely punctulate; marginal stria joining outer subhumeral; first dorsal stria very fine, complete; second stria very fine, reaching middle; epipleurae rugose, with short apical segment of stria (fig. 26).

Propygidium with dense setigerous punctures, pygidium more sparsely punctate.

Prosternal lobe at lower level than keel, both rugose and finely setose; prosternal lobe bisinuate, with medial depression (fig. 38); apical 2/3 of inner prosternal striae indistinct, remainder fine; outer prosternal striae very fine or obsolete. Mesosternum wide; meso-metasternal excavation deep; without lateral foveae. Metasternum finely and densely punctulate, with microsetae; inner stria not reaching metacoxae; sides fossulate.

First abdominal sternite finely and densely punctulate.

Legs long and very expanded.

Male unavailable.

Length 2.5 mm. Width 2.3 mm.

Type material

Only known by the holotype ♀ [in MNHN] labelled: /Type/, /*Sternocoelis robustus* Pic/, /Libadia, Chypre/.

Distribution

It is known only from the type locality, Cyprus island.

Ecology

No biological data are available.

Sternocoelis fuscus (Schmidt, 1888)

(Figs 10, 39, 60 and 76)

Hetaenius fuscus Schmidt, 1888: 238.

Sternocoelis mauritanicus Lewis, 1888a: 152 (nov. syn.).

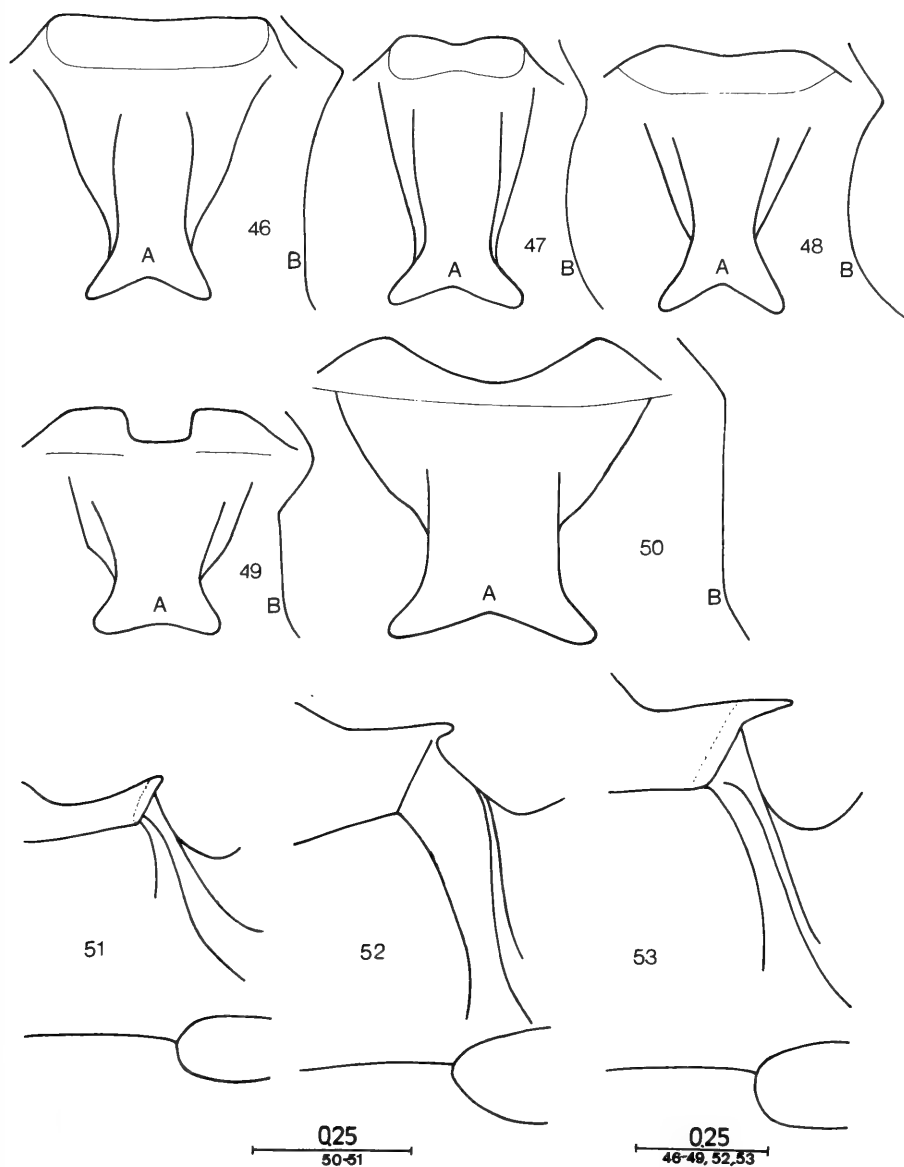
Sternocoelis fuscus (Schmidt): Lewis, 1888a: 152.

Sternocoelis aureopilosus Escalera, 1921: 128 (nov. syn.).

Sternocoelis incisus ssp. *mendizabali* Cobos, 1949: 578 (synonymized by Yélamos, 1993: 155).

RE-DESCRIPTION

Colour reddish brown, shiny; body weakly convex, broadly oval; covered with long setae, longer on margins and propygidium.



FIGS 46-53

Prosternal lobe and keel, ventral view (A), outline (B): *S. hispanus* (Rosenhauer) (46); *S. arachnoides* (Fairmaire) (47); *S. slaoui* Théry (48); *S. comosellus* (Fairmaire) (49); *S. espadaleri* n. sp. (50). Left half of mesosternum and metasternum: *S. vaucheri* Lewis (51); *S. merklia* (Schmidt) (52), *S. bedeli* (Lewis) (53). Scale in mm.

Frons rugose; frontal stria cariniform, irregular, crossing epistoma; labrum with medial depression; mandibles large and convex; antennal scape very enlarged and rugose.

Pronotum subtrapezoidal (fig. 10); densely punctate on sides and apical margin, anterior angles wide, slightly elevated, and posterior angles produced; pronotal base with an impression near first and second dorsal striae; marginal stria complete. Elytra weakly convex, finely and densely punctulate; first dorsal stria complete; second stria reduced apically; third stria only reaching middle; outer subhumeral stria joined to marginal; epipleurae rugose, with a stria parallel to marginal stria.

Propygidium and pygidium coarsely and densely punctate.

Prosternum with lobe clearly bisinuate, prominent, rugose, separated from keel by a shallow depression (fig. 39); keel with inner striae strong, not joined in front, rugosely punctate between; outer striae strong. Meso-metasternal excavation deep; mesosternum with fine oblique impressions next to mesocoxae. Metasternum finely punctate, with three fine lateral striae, the inner reaching near to metacoxae; sides fossulate.

First abdominal sternite strongly and densely punctate on disc, coarser and denser on sides.

Legs very expanded; meso- and metatibiae triangular (fig. 60); rugose, with short yellow setae.

Aedeagus as figure 76.

Length 1.4-1.7 mm. Width 1.3-1.5 mm.

Type material

The holotype ♀ of *Haeterius fuscus* Schmidt has been studied [in MNHU]: /Type/, /Andalusia/, /coll. J. Schmidt/, /fuscus Schmidt/, /Zool. Mus. Berlin/.

The holotype ♀ of *Sternocoelis mauritanicus* Lewis has been studied [in NHML]: /*Hetaerius mauritanicus* Lewis, Type/, /Type/, /Tangier, Lewis, 9.4.88/, /G. Lewis Coll., B.M. 1926-369/.

Four specimens of the type series of *Sternocoelis aureopilosus* Escalera have been examined. The lectotype and three paralectotypes are designated. LECTOTYPE [in MNCN] labelled: /Larache, M. Escalera/, /*Sternocoelis aureopilosus* Escalera, typ./.

PARALECTOTYPE [all in MNHN] labelled: (1) /Larache/, /Type/, /Type qui a servi à Escalera pour faire son dessin/, /*Sternocoelis aureopilosus*, Type, Esc./, /Coll. Dr. V. Auzat/, /*Sternocoelis aureopilosus* Esc./; (2) /Larache, 12.1.1921/, /Coll. Dr. V. Auzat/, /Paratype/, /*Sternocoelis aureopilosus* Esc./; (3) /Larache/, /Paratype/, /*Sternocoelis aureopilosus* Esc./.

The holotype ♀ of *Sternocoelis incisus mendizabali* Cobos was also studied [in the EEZA]: /*Sternocoelis incisus* ssp. *mendizabali* nov., Cobos Sánchez Det. 1949/, /Torremolinos, Málaga, (Hispania), Cobos Sánchez/, /Holotipo/.

Other material examined

Two specimens of the MHNG labelled as follows: (1) /Tanger, Olcese/; (2) /Lalla Mimouna, 8-3-62/, /Maroc, leg. R. Mussard/, /J. Théron det., 1963, *Eretmotus* sp. ? du groupe *ibericus* Bris./.

Five specimens of the MNCN: (1) /Tanger, M. Escalera/; (2) /1897 Tanger/; (3) /10.906, Tanger/, /*S. mauritanicus* Law./; (4) /Marruecos, Tanger, VI-1905 Escalera/; (5) /Hontanares, Hispania, IV-50, M. Escalera/, /*Sternocoelis incisus* Schm./.

Five specimens of the MNHN: (1 and 2) /Larache/, /Coll. Dr. V. Auzat/, /*Sternocoelis mauritanicus* Lew./; (3) /3.95, Tanger/, /Maroc, ex Musaeo, H. Vaucher 1908/, /*Sternocoelis*

mauritanicus;/ (4) /Tanger, Maroc;/ (5) /Larache/, /Maroc, ex Escalera/, /Coll. Dr. V. Auzat/, /*Sternocoelis mauritanicus* Lew./.

Five specimens of the NHML, four of them labelled /1897, Tanger/, /Vaucher/, /G. Lewis Coll., B.M. 1926-369/ the fifth /4.95, Tangier/ with the same last label.

Two specimens in TY: (1) /Algeciras;/ (2) /Koumch (circa Beni Mellal MA.), 1200 m, 17-V-84, X. Espalader leg./, /*Sternocoelis alluaudi*, Théry, J. de Ferrer det. 1986/.

Distribution

This species has a wide distribution area with scarce localities. It is mainly known from the south of Spain (Andalusia) and north of Morocco (Tangier and Larache). It was also recorded by WALKER (1889) from Gibraltar. There are additional records from Hontanares (Segovia, central Spain) and Beni-Mellal, Morocco).

Ecology

A clear cline exists for several morphological characters, the specimens from central Spain being very different from those of central Moroccan origin.

They have been collected in winter and spring at low and mid elevations. In Morocco they have been found in nests of *Aphaenogaster gemella* ssp. *maroccana* Forel.

Sternocoelis incisus (Schmidt, 1885)

(Figs 11, 40 and 77)

Hetaerius incisus Schmidt, 1885b: 440.

Sternocoelis incisus (Schmidt): Lewis, 1888a: 155.

Haeterius cruzi Escalera, 1929: 375 (synonymized by Yélamos, 1993: 156).

Haeterius cruzi var. *micropilosus* Escalera, 1929: 378 (synonymized by Yélamos, 1993: 156).

Sternocoelis cruzi (Escalera): Mazur, 1984: 326.

RE-DESCRIPTION

Colour dark brown, shiny; body weakly convex, broadly oval; covered with short setae, longer on margins.

Frons coarsely and densely punctate; frontal stria cariniform, irregular, crossing epistoma; labrum truncate, with shallow medial depression; mandibles large, convex, rugose; antennal scape strongly enlarged, rugose, with short setae.

Pronotum with broad, slightly elevated anterior angles; posterior angles produced (fig 11); pronotum with basal impression opposite to first and second dorsal striae: marginal stria complete; sides parallel; strongly and densely punctate, sparser on disc. Elytra weakly convex, expanded, finely and densely punctulate; first dorsal stria complete; second stria slightly surpassing middle; third stria shorter; outer subhumeral stria strong, cariniform, joined to fine and irregular marginal stria; epipleurae rugose, with short setae and a short irregular stria.

Propygidium and pygidium with dense setigerous pores.

Prosternum with broad keel; inner striae strong, prominent near depression and prolonged to it; between both inner striae there is a strongly and densely punctate

depression; depression between lobe and keel very deep (fig. 40); lobe prominent, rather rugose, setose; outer striae short and strong. Meso-metasternal excavation deep; sides mesosternum with narrow and deep lateral foveae, near metacoxae. Metasternal disc nearly smooth, rather depressed; lateral striae of metasternum fine; both inner striae long, not reaching metacoxae, outer stria shorter and evanescent.

First abdominal sternite convex; disc smooth; sides with large punctures.

Legs very expanded; meso- and metatibiae triangular, with dense punctures and setae.

Aedeagus as figure 77.

Length 1.8-2.1 mm. Width 1.4-1.7 mm.

Type material

The holotype ♀ of *Hetaerius incisus* Schmidt [in MNHU] has been examined. It is labelled: /Type/, /*incisus* typ. Schmidt/, /Hispania/, /coll. J. Schmidt/, /*incisus* Schmidt/.

The lectotype and one paralectotype of *Haeterius cruzi* Escalera have been studied [in MNCN]. Lectotype ♂ labelled: /Cercedilla, C. Bolivari/, /*St. Cruzi* typ. Esc./, Paralectotype ♀: /Escorial, 20.5.1926/, /*St. Cruzi* Esc./.

The lectotype and 10 paralectotypes of *Haeterius cruzi* var. *micropilosus* Escalera have been studied [in MNCN]. Lectotype ♂ labelled: /Escorial, 14.5.1926/, /*St. cruzi* var. *micropilosus* Esc./ [in MNCN]. Paralectotypes: two ♀♀ with the same labels as the lectotype [in MNCN and MNHN]; four ♂♂ and four ♀♀ labelled: /Escorial, 20.5.1926/ [seven in MNCN and one in MNHN].

Other material examined

Three specimens of the DEI have been studied. Two specimens labelled: /Hispan./, /Coll. Franklin Müller/, /*Sternocoelis Marseulii* Bris./, One specimen labelled: /Sr. Espuna, Hisp. mer. Ehlers/, /syntypus/, /*incisus* Schmidt/, /Coll. L. v. Heyden DEI Eberswalde/.

Distribution

Few records exist for this species and their distribution is therefore poorly known. *S. incisus* is known to occur in the mountains of central and south-eastern Spain (Sierra del Guadarrama, Madrid and Sierra de Espuña, Murcia).

Ecology

Specimens have been found mainly in spring. *S. incisus* inhabits nests of several species of *Aphaenogaster*.

Sternocoelis alluaudi Théry, 1921

(Figs 12 and 24)

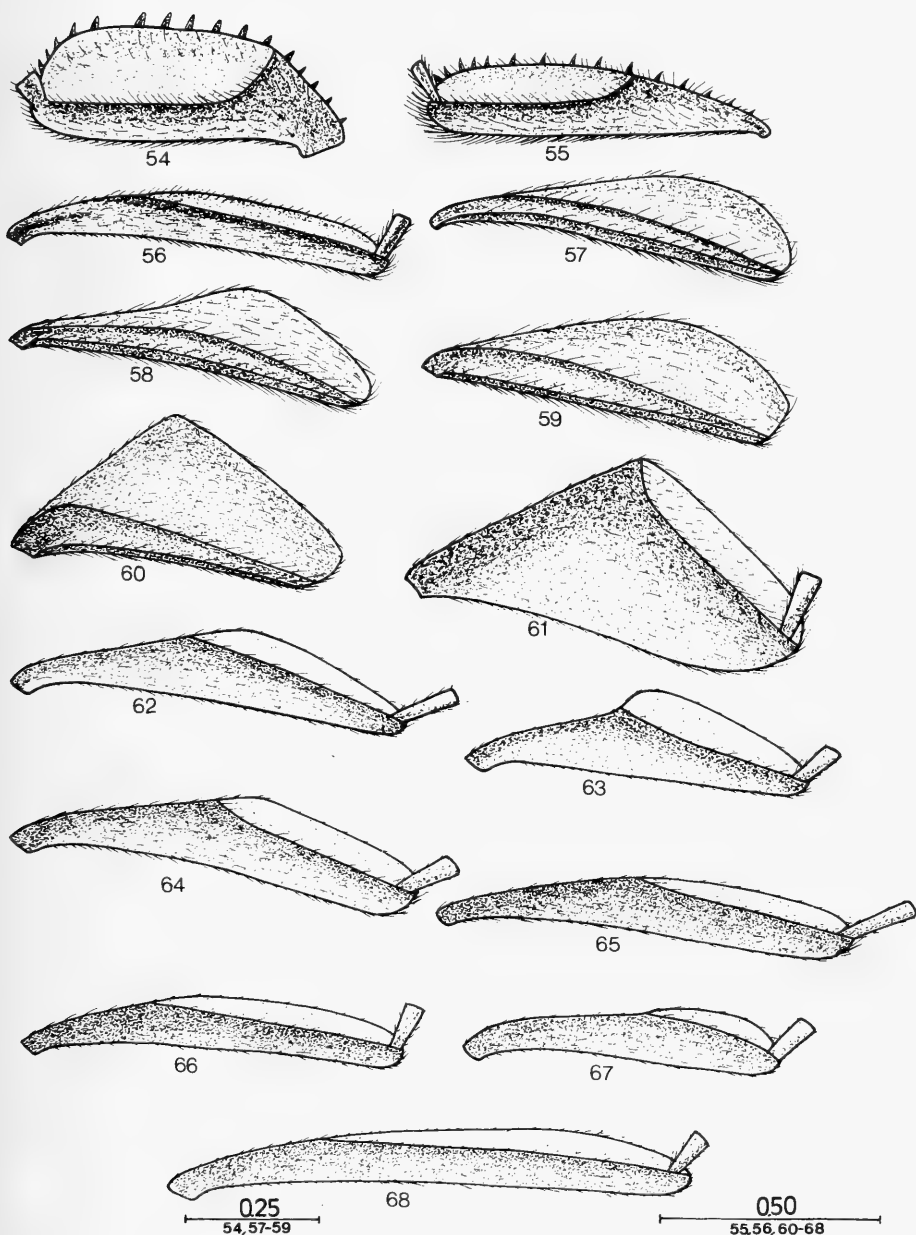
Sternocoelis alluaudi Théry, 1921: 19.

Sternocoelis variolosus Théry, 1921: 20 (nov. syn.).

Sternocoelis loustali Kocher, 1956: 367 (nov. syn.).

RE-DESCRIPTION

Colour reddish brown, shiny; body weakly convex; with short and sparse setae laterally and on legs.



FIGS 54-68

Right protibia, inner side: *Sternocoelis marseulii* (Brisout de Barneville) (54); *S. arachnoides* (Fairmaire) (55). Right mesotibia, inner side: *S. slaoui* Théry (56). Left metatibia, outer side: *S. otini* Peyerimhoff (57); *S. marginalis* Normand (58); *S. grandis* (Reitter) (59); *S. fuscus* (Schmidt) (60). Right metatibia, inner side: *S. acutangulus* (Lewis) (61); *S. atlantis* Théry (62); *S. setulosus* (Reitter) (63); *S. hispanus* (Rosenhauer) (64); *S. arachnoides* (Fairmaire) (65); *S. slaoui* Théry (66); *S. comosellus* (Fairmaire) (67); *S. espadaleri* n. sp. (68). Scale in mm.

Frons rugose, depressed, and sparsely setose; frontal stria cariniform, interrupted on epistoma; labrum long, smooth; mandibles convex, stout, punctate on lateral area, glabrous; antennal scape very enlarged (fig. 24), rugose, with scarce setae.

Pronotum convex, coarsely, densely punctate, punctures regularly distributed; marginal stria distinct; anterior angles truncate (fig. 12), slightly elevated; posterior angles gradually produced; with shallow depression near posterior angles. Elytra rather expanded, subparallel; surface coarsely and densely punctate; first dorsal stria complete; second stria slightly surpassing middle, third stria shorter; outer subhumeral stria complete, joined to marginal stria; epipleurae somewhat rugose, without striae.

Propygidium and pygidium coarsely, densely punctate and setose.

Prosternum rugose, with short setae; prosternal lobe at right angle in relation to keel in lateral view; with deep depression between keel and lobe; inner prosternal striae cariniform, very prominent and wide, sinuate, forming a medial projection; outer striae cariniform. Meso-metasternal excavation very wide and deep; lateral foveae deep. Metasternum finely punctulate on disc, fossulate on sides; inner lateral stria short, only reaching middle, both outer striae approaching, almost reaching metacoxae.

First abdominal sternite finely punctulate.

Legs very short and very expanded, densely punctate and setose.

Aedeagus morphology typical of the genus.

Length 1.7-1.9 mm. Width 1.4-1.5 mm.

Type material

Three specimens of the type series of *Sternocoelis alluaudi* Théry have been examined (accompanied with ants). The lectotype and two paralectotypes are now designated. LECTOTYPE labelled: /Ain Leuh, 112/, /Type/, /*Sternocoelis alluaudi* Théry/, /Type/, [in MNHN]. PARALLECTOTYPES labelled: (1) /Ain Leuh, 1500 m, Alluaud 84/, /*Sternocoelis alluaudi*, Théry/, /Vendu par Théry au 1938/, /Type/ [in MNHN]; (2) /M. Atl., Maroc, Coll. Théry/, /*Alluaudi* Théry/, /Cotype/ [in MNCN].

The holotype of *Sternocoelis variolosus* Théry [in MNHN] was also studied labelled as follows: /Dradek près Rabat, Alluaud 63/, /*Sternocoelis variolosus*, Type, Théry/, /Type/ (accompanied with an ant).

The holotype of *Sternocoelis loustali* Kocher has not been loaned by the Institut Scientifique Chérifien from Rabat. On the basis of the description, I regard it as a new synonym.

Other material examined

Seven specimens of the MNCN have been examined, labelled as follows: (1 and 2) /Iguermalen, Targuist, Rif, VI-1930, Exp. C. Bolivar/; (3) /Iguermalen, Beni Mesdui, VI-1932, M. Escalera/; (4) /Imasinen, Beni Seddat, Rif, VI-1930, Exp. C. Bolivar/; (5) /Bab Chiquer, Ketama, Rif, VI-1932, M. Escalera/; (6 and 7) /Azrou, 5 Mai 29, A. Théry/.

Three specimens of the MNHN were also seen and labelled: (1) /Bou Chaut, Maroc, Coll. Théry/, /Coll. Dr. V. Auzat/, /*Sternocoelis alluaudi* Théry, Théry det./; (2) /Azrou, 5 Mai 29, A. Théry/, /voir *acutangulus* Lewis/; (3) /Daïet Ifrane/, /*St. acutangulus* Lew. 22/.

One specimen was examined of the TY labelled: /Dayet Ifrah, Marruecos, 1750 m, P. Rotraw leg./.

Distribution

S. alluaudi is known from the Moyen-Atlas and Rif mountains, and from the environs of Salé, Morocco.

Ecology

This species inhabits the nests of *Aphaenogaster* sp., mainly in mountainous areas. It is active from late spring to early summer.

***Sternocoelis acutangulus* (Lewis, 1887)**

(Figs 13, 41, 61 and 85)

Hetaerius acutangulus Lewis, 1887: 164.

Sternocoelis acutangulus (Lewis): Lewis, 1888a: 146.

RE-DESCRIPTION

Colour reddish brown, shiny; body weakly convex and stout; covered with short yellow setae.

Frons with coarse and dense punctures; frontal stria cariniform, irregular, evanescent on epistoma; labrum with a shallow impression; mandibles large, convex, densely punctate; antennal scape greatly enlarged and rugose.

Pronotum convex, with anterior angles slightly elevated; posterior angles strongly produced (fig. 13); sides parallel; base of pronotum with impression near base of first dorsal stria; marginal stria partially evanescent; surface densely covered with large shallow punctures, irregular and rugose on anterior angles of pronotum. Elytra strongly expanded, weakly convex; surface with mixture of dense punctures, setigerous pores, and other smaller punctures; first dorsal stria complete; second stria shortened apically; third stria reaching middle; outer subhumeral stria very long, well impressed, curved toward epipleurae at apical half; marginal and outer subhumeral striae joined; epipleurae rugose, with short setae, lacking striae.

Propygidium and pygidium with dense setigerous pores.

Prosternum strongly rugose; inner striae well impressed, with wide projections near to depressed zone; depression between lobe and keel deep and narrow (fig. 41); these striae converge on depressed part; prosternal lobe less prominent than projections of inner striae; outer prosternal striae short and well impressed. Meso-metasternal excavation very deep; sides mesosternum with deep and wide lateral foveae. Metasternum finely punctulate; inner lateral stria fine, reaching middle of prosternum, median stria are stronger and longer, very oblique, not reaching metacoxae, very fine and short the outer stria; sides fossulate.

First abdominal sternite finely and densely punctate, with coarser punctures on sides.

Legs long, strongly expanded, rugose and setose; meso- and metatibiae triangular (fig. 61).

Aedeagus morphology typical; spiculum gastrale as in figure 85.

Length 1.8-2.4 mm. Width 1.4-2.1 mm.

Type material

The type series containing a lectotype and four paralectotypes have been examined [all in NHML]. Lectotype, a ♂ labelled: /Tangier, Lewis, 8.4.88/, /G. Lewis Coll. B.M. 1926-369/. Paralectotypes, a ♀ with the same first and second labels, moreover /*Hetaerius acutangulus*

Type, Lewis/. Two ♀♀ and a ♂ (all accompanied by ants) with the same first and second labels, moreover */Sternocoelis acutangulus/*.

Other material examined

Four specimens of the DEI labelled: (1 and 2) /Maroc/, /Coll. Stierlin/, */S. acutangulus Lewis/*; (3) /Marocco, Coll. O. Leonhardt/, */Sternocoelis acutangulus Lewis/*; (4) /1897, Tanger/, */acutangulus Fairm., Tanger Desbr./*, /Coll. L. v. Heyden, DEI Eberswalde/.

Five specimens of the MNCN labelled: (1 and 2) /1897 Tanger/, */S. acutangulus Lewis/*; (3) /Iguermalen, Targuist, Rif, VI-1930 Exp. C. Bolivar/; (4 and 5) /Larache, M. Escalera/, /MNCN Madrid/.

Nineteen specimens of the MNHN labelled: (1) /Tanger, Lewis, 8.4.88/, */acutangulus, Lewis 89, Tanger/*; (2) /3.44, Tanger/; (3) /Tanger/; (4) /1897, Tanger/; (5) /Larache/, /Ex. typique qui a servi à Escalera pour faire son dessin/, /Coll. Dr. V. Auzat/, /Type/, */Sternocoelis acutangulus Lew./*; (6, 7, 8, 9 and 10) /Larache/, /Maroc, ex Escalera/, /Coll. Dr. V. Auzat/, /Paratype/, */Sternocoelis acutangulus Lew./*; (11) /6.94, Tanger/, */acutangulus/, /Sternocoelis acutangulus Lew./*; (12) /Maroc, ex Musaeo, H. Vaucher 1908/, */Sternocoelis acutangulus Lew./*; (13 and 14) /Larache, Maroc/, */Sternocoelis acutangulus Lew./*; (15) /Gibraltar, ex Coll. Bonnaire/, */Gibraltar/, /acutangulus Lewis, ex ipso/, /Coll. Dr. V. Auzat/, /Sternocoelis acutangulus Lew./*; (16) */Sternocoelis acutangulus/, /Tanger, Lewis, 10-4-88/, /Muséum Paris, Coll. de Marseul, 1890/, /Hetaerius acutangulus Lewis/*; (17) /5.95, Tangier/, */Lewis det./, /Muséum Paris, 1933, Coll. Desbordes/, /acutangulus Lewis/*; (18) /Maroc, E. Tisson/, /Muséum Paris, 1933, Coll. Desbordes/, */Sternocoelis acutangulus, Peyer. det. 1914/*; (19) /Gibraltar, J.J. Walker/, */Sternocoelis acutangulus Lew./*.

Seven specimens (accompanied by ants) of the NHML labelled as follows: (1) /Tangier, Lewis, 9-4-88/, /G. Lewis Coll., B.M. 1926-369/ (all the specimens contain this label); (2) /Tangier, (Olcese), 1896/; (3) /Tangier, (Lewis), 31.3.88/, */Sternocoelis acutangulus Lewis/*; (4) /Tangier, Lewis, 4.4.88/; (5 and 6) /Tangier, 5.95/, */Sternocoelis acutangulus Lewis/*; (7) /Gibraltar, J.J. Walker/.

Two specimens of the NHMW: /Tanger, Herrmann/.

Five specimens of the TM, four of them labelled /Gibraltar, J.J. Walker/, */Sternoc. acutangulus Lew., Coll. Reitter/* and one more specimen labelled /Tangier, Lewis, 9.4.88/ and the same second label.

Four specimens of TY all labelled /Tanger 1897/, */Sternocoelis acutangulus Lewis/*.

Distribution

The species occurs in northern Morocco (Tangier and Rif regions) and southern Iberian Peninsula (only known from Algeciras, Cádiz, and Gibraltar). It is very common in and around Tangier.

Ecology

S. acutangulus is active in winter and spring at low and middle elevations. In Morocco the species inhabits nests of *Aphaenogaster sardoa* Mayr.

Sternocoelis pluristriatus (Fairmaire, 1877)

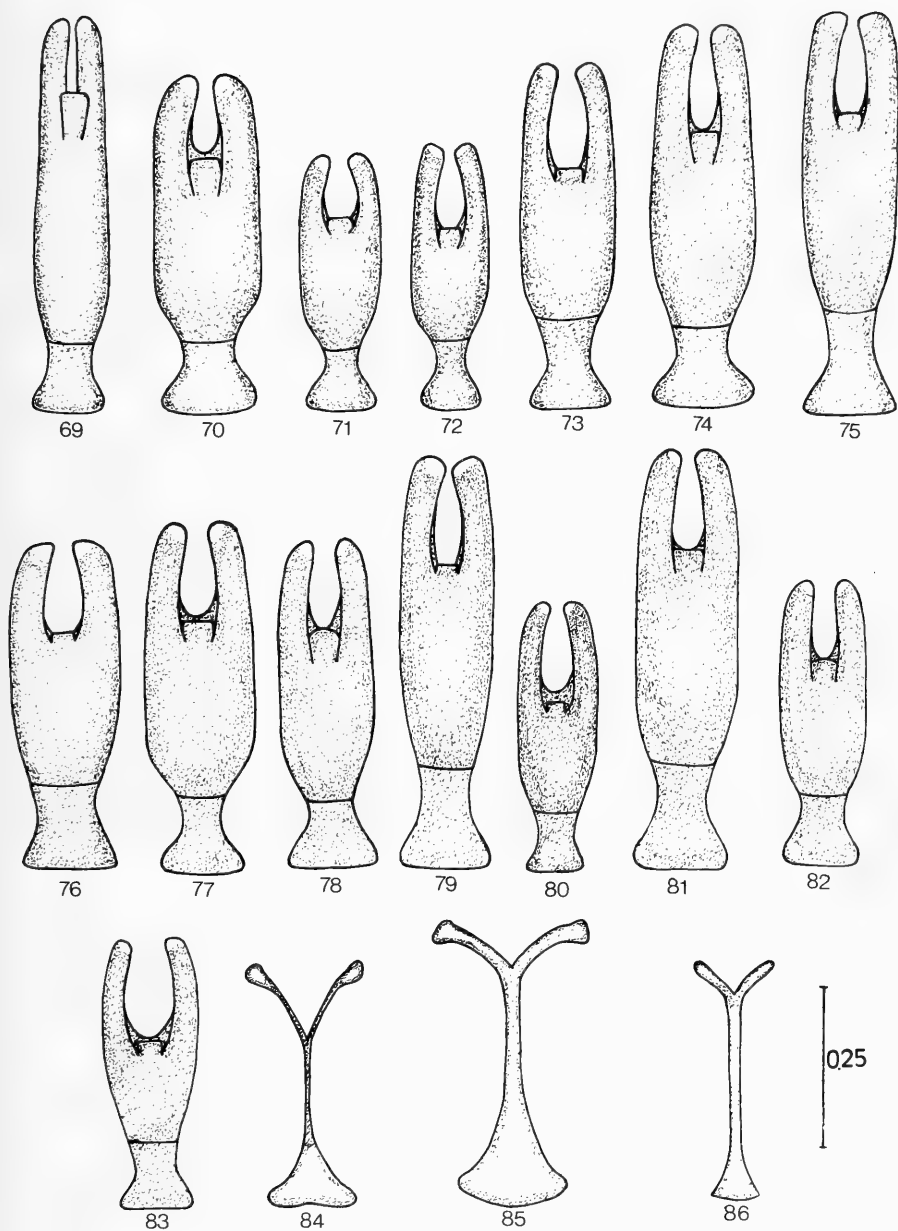
(Fig. 14)

Hetaerius pluristriatus Fairmaire, 1877: 98.

Sternocoelis pluristriatus (Fairmaire): Lewis, 1888a: 151.

RE-DESCRIPTION

Colour light brown, shiny; body weakly convex; covered with yellow medium-length setae.



FIGS 69-86. Aedeagus in dorsal view: *Hetaerius ferrugineus* (Olivier) (69); *Sternocoelis viaticus* Lewis (70); *S. marseulii* (Brisout de Barneville) (71); *S. vaucheri* Lewis (72); *S. puberulus* (Motschulsky) (73); *S. merklII* (Schmidt) (74); *S. laevidorsis* (Fairmaire) (75); *S. fuscus* (Schmidt) (76); *S. incisus* (Schmidt) (77); *S. bedeli* (Lewis) (78); *S. setulosus* (Reitter) (79); *S. hispanus* (Rosenhauer) (80); *S. arachnoides* (Fairmaire) (81); *S. comosellus* (Fairmaire) (82); *S. espadaleri* n. sp. (83). Spiculum gastrale in dorsal view: *S. marseulii* (Brisout de Barneville) (84); *S. acutangulus* (Lewis) (85); *S. espadaleri* n. sp. (86). Scale in mm.

Frons finely rugose; frontal stria cariniform, irregular, evanescent on epistoma; labrum flat and truncate; mandibles large, convex, punctate; antennal scape very enlarged and rugose.

Pronotum subtrapezoidal, weakly convex; anterior angles truncate and slightly elevated; posterior angles not produced (fig. 14); marginal stria fine and complete; surface finely, sparsely punctate, chiefly on disc; shallow depression opposite to base of second dorsal stria. Elytra weakly convex, with irregular and dense punctures; first dorsal stria complete; second stria reaching apical 2/3; third stria on anterior half; fourth stria as an anterior arch; outer subhumeral stria complete, joined to marginal at middle; epipleurae rugose and without striae.

Propygidium coarsely and densely punctate. Pygidium less densely punctate.

Prosternum with lobe and keel at about the same level, rugose and with short setae; prosternal lobe bisinuate; outer prosternal striae well impressed; inner striae strong, with a projection on apical 2/3, then finer (prosternal lobe and keel like *S. punctulatus*). Meso-metasternal excavation deep; mesosternum with deep lateral foveae. Metasternum with disc finely punctulate; sides coarsely and irregularly punctate; striae distinct, inner short, outer striae long.

First abdominal sternite finely punctulate.

Legs short, stout, setose; meso- and metatibiae very expanded, triangular.

Aedeagus with the common morphology.

Length 1.5-1.6 mm. Width 1.2-1.3 mm.

Type material

Three specimens from the type series have been examined. The lectotype and two paralectotypes are now designated. LECTOTYPE labelled: /Daya/, /Type/, /*pluristriatus*/ [in MNHN]. PARALECTOTYPES labelled: (1) /exemplaire typique, *pluristriatus*, Daya Taiza/ [in MNHN]; (2) /Type/, /Daya, Bedel/, /exemplaire typique/, /Coll. J. Schmidt/, /Zool. Mus. Berlin/, /*pluristriatus* Fairm./ [in MNHU].

Other material examined

Eight specimens (accompanied by ants) from the MNHN labelled as follows: two specimens without labels in collection Desbordes; five specimens labelled /Bou Berak près Dellys, Algérie/, /*Sternocoelis pluristriatus*/; one specimen with the two same labels as well as /comparé au Type (Coll. Bedel) 11-7e-28 Auzat/ and /Coll. Dr. V. Auzat/.

Distribution

This species is only known from Dhaya (Tlemcen region) and Dellys, north of Algeria.

Ecology

S. pluristriatus is active in spring and inhabits the nests of *Aphaenogaster* sp. at middle altitude.

Sternocoelis bedeli (Lewis, 1884)

(Figs 15, 42, 53 and 78)

Hetaerius bedeli Lewis, 1884: 83.

Hetaerius politus Schmidt, 1888: 237 (nov. syn.).

Sternocoelis cancer Lewis, 1888a: 147 (nov. syn.) (synonymized of *S. politus* by Lewis, 1894: 150).

Sternocoelis bedeli (Lewis): Lewis, 1888a: 147.

Sternocoelis extructisternum Lewis, 1888a: 150 (nov. syn.).

Sternocoelis pectoralis Lewis, 1888a: 152 (nov. syn.).

Sternocoelis politus (Schmidt): Lewis, 1888a: 154.

Sternocoelis sedilloti Lewis, 1889: 285 (nov. syn.) (synonymized of *S. politus* by Lewis, 1894: 150).

RE-DESCRIPTION

Colour dark brown, shiny; body weakly convex; with irregularly spaced yellow erect mid-length setae, sometimes lacking or dense on pronotum, elytra and prosternum, with or without dense setae.

Frons finely rugose; frontal stria cariniform, evanescent on epistoma; labrum slightly depressed; mandibles large, convex, densely punctate; antennal scape very enlarged, rugose, with short setae.

Pronotum weakly convex anteriorly, sometimes with setae; anterior angles truncate, slightly elevated, and posteriorly produced (fig. 15); marginal stria complete; sides not parallel; surface densely punctured on anterior half, smaller and sparsely punctulate on remainder. Elytra not parallel, strongly enlarged on shoulders; densely punctate, without setigerous pores; first dorsal stria complete, second slightly longer than half, and third as a short anterior trait; outer subhumeral and marginal striae approaching medially, not united; epipleurae rugose, without striae.

Pygidium with coarse and dense setigerous punctures. Pygidium similarly punctate, but less densely so.

Prosternal lobe and keel at same level, rugose and setose; lobe emarginate; prosternal striae strongly impressed, the inner very distant, with medial projections (fig. 42). Meso-metasternal excavation deep; mesosternum with very deep lateral foveae. Metasternum with inner lateral stria fine and short, medial and outer very oblique, almost reaching metacoxae (fig. 53); disc finely and densely punctulate; sides with irregular and dense punctures.

First abdominal sternite finely and densely punctulate.

Legs very robust, with tibiae very expanded, punctate and setose.

Aedeagus as figure 78.

Length 1.7-2.1 mm. Width 1.5-1.8 mm.

Type material

Two specimens of the type series of *Hetaerius bedeli* Lewis have been examined (series originally composed by three specimens). The lectotype and one paralectotype are now designated. LECTOTYPE labelled: */Hetaerius Bedeli* Lewis, Type/, /Type/, /Recd. from Bedel 7-4-84/, /Daya, XI.75/, /G. Lewis Coll., B.M. 1926-369/ [in NHML]. PARALECTOTYPE: /Type/, /Daya, XI.75/, /exemplaire typique/, /Coll. J. Schmidt/, /Zool. Mus. Berlin/, */Bedeli* Lewis/.

Three specimens of the type series of *Hetaerius politus* Schmidt have been examined. The lectotype and two paralectotypes are now designated. LECTOTYPE labelled: /Type/, /Edough/, /Coll. J. Schmidt/, /Zool. Mus. Berlin/, */politus* Schmidt/ [in MNHU]. PARALECTOTYPES two specimens labelled /Edough, coll. Bonnaire/, /Edough/, /Type/, */Hetaerius politus* Schmidt, Type/, */Sternocoelis politus* Schm./.

Sixteen specimens of the type series of *Sternocoelis cancer* Lewis have been examined. The lectotype and 15 paralectotypes are now designated. LECTOTYPE labelled: */Sternocoelis*

cancer, Lewis Type/, /H. Rirha Lewis, 27.2.88/, /Type/, /G. Lewis Coll., B.M. 1926-369/ [in NHML]. PARAELECTOTYPES: ten specimens /Hamman Rirha, (Lewis), 6.3.88/, /*S. cancer* Lewis/ and the same last label [in NHML]; one specimen /Hamman Rirha, Lewis, 26.2.88/, /*Sternocoelis cancer* Lewis/ and the same last label [in NHML]; one specimen /H. Rirha, 27.2.88, Lewis/ and the same two last labels [in NHML]; one specimen /H. Rirha, Lewis/, /Type/, /Coll. Bonnaire/, /Coll. Dr. V. Auzat/, /*Sternocoelis cancer* Lewis/ [in MNHN].

The holotype of *Sternocoelis extructisternum* Lewis has been studied, labelled as follows: /*Hetaerius extructisternus*, Lewis, Type/, /Coll. Mouchicourt 1879/, /Algeria/, /Type/, /G. Lewis Coll., B.M. 1926-369/ [in NHML].

The holotype of *Sternocoelis pectoralis* Lewis has been studied, labelled: /*Hetaerius pectoralis*, Lewis, Type/, /Tlemcen, Lewis, 21.3.88/, /G. Lewis Coll., B.M. 1926-369/ [in NHML].

I was not able to study the type series of *Sternocoelis sedilloti* Lewis. Instead I examined one specimen compared with the type by Lewis (see below).

Other material examined

Two specimens of the DEI labelled as follows: (1) /Coll. Kraatz/, /Bickhardt det./, /*Sternocoelis cancer* Lew./; (2) /Hamman/, /Coll. Kraatz/, /Bickhardt det./.

One specimen of the MHNG labelled as follows: /Bougie, Kabylie, L. Puel/, /*politus*/.

Seventeen specimens of the MNHN labelled as follows: (1) /Mt. Babor, Algérie/, /*Sternocoelis cancer* Lew./; (2) /Bougie, L. Coutazar/, /Coll. Dr. V. Auzat/, /*Sternocoelis politus* Schm./; (3) /Bou Berak près Dellys, Algérie/, /Coll. Dr. V. Auzat/, /*Sternocoelis politus* Schm./; (4) /Kurota, mai 1901/; (5) /*cancer*/, /*Sternocoelis cancer* Lew., Lewis 99, Cirta 3.5.1894/; (6) /St. Charles, Algérie, A. Théry/, /4.3.91/; (7) /El Routerez, Algérie, Coll. Théry, 17.3.94/, /*politus* Sch. (*cancer* Lewis)/; (8) /Oued Chesp, L. Clouet des Pesrouches à Medjez-Amar, Algérie/; (9) /Mt. Babor, 1901, Vauloger/; (10 and 11) /Bugeaud, L. Clouet des Pesrouches à Medjez-Amar, Algérie/; (12) /Mt. Babor, Algérie, Coll. Théry/; (13) /Sidi Abdelkalai, Blida, 16.4.1914/; (14) /Medjez-Amar, Algérie, L. Clouet des Pesrouches/, /*Sternocoelis politus*/; (15) /Coll. Bickhardt/, /Muséum Paris, 1933, Coll. Desbordes/, /*Hetaerius cancer* Lewis/; (16) /Bou Berak près Dellys, Algérie/, /*Sternocoelis pectoralis* Lew./; (17) /*Sternocoelis* Lew. 88/, /Mt. Rirha, Lewis/, /Muséum Paris, Coll. de Marseul, 1890/, /*Hetaerius Bedeli* Lewis/.

Seven specimens of the MNHU labelled: (1 and 2) /H. Rirha, Lewis/, /*Hetaerius Bedeli* Lewis/, /Zool. Mus. Berlin/ (all the specimens with this label); (3, 4 and 5) /Meskoutin, 8.4.92/, /*Sternocoelis Cancer* Lewis/; (6) /Cirta, 3.5.94/, /*Sternocoelis cancer* Lewis/, /69562/; (7) /H. Rirha, Lewis/, /*cancer* Lewis/.

Sixteen specimens of the NHML: (1) /Constantine, 28.3.92/, /*Sternocoelis Sedilloti* Lewis, compared with Type, 15.5.92/, /G. Lewis Coll., B.M. 1926-369/ (the fifteen first specimens with this label); (2 and 3) /Kabylie 1897/, /Yakouren/, /*S. bedeli* Lew./; (4) /Cirta, 2.5.94/, (5) /Frenda, Oran, Lutand/; (6) /Algiers, Bois de Bol, 9.5.92/, /*Sternocoelis cancer* Lewis/; (7, 8 and 9) /Cirta, 3.5.94/; (10 and 11) /Cirta, 2.6.94/; (12) /Blida, 28.4.92/; (13, 14 and 15) /Meskoutin, 8.4.92/; (16) /Sharp Coll., 1905-3.3/, /*S. cancer* Lew./.

One specimen of the TM: /H. Rirha, Lewis/, /*Sternoc. cancer* Lew., Coll. Reitter/.

Ten specimens of the TY, five of them labelled /Bou Berak, près Dellys, 6-11 Mai 1901, Dr. A. Chobaut/, /*punctulatus*/.

Distribution

S. bedeli is the most common species in northern Algeria, from Tlemcen to Annaba.

Ecology

This species is active from November to June at low and middle altitude. It inhabits the nests of *Aphaenogaster canescens* Emery and *A. depilis* Santschi.

***Sternocoelis punctulatus* (Lucas, 1855)**

(Figs 16 and 43)

Hoeterius punctulatus Lucas, 1855: 4 (error).*Sternocoelis punctulatus* (Lucas): Lewis, 1888a: 154.*Hetaerius cavisternus* Marseul, 1862: 713 (synonymized by Lewis, 1888a: 154).*Hetaerius lioderus* Fairmaire, 1877: 98 (synonymized by Lewis, 1888a: 154).**RE-DESCRIPTION**

Colour reddish brown, shiny; body weakly convex; with long yellow, aligned and reclinate setae.

Frons with small setigerous punctures; frontal stria cariniform, evanescent on epistoma; labrum flat, truncate; mandibles large, convex, finely punctulate; antennal scape very enlarged, rugose and setose.

Pronotum trapezoidal, with anterior angles wide, truncate and slightly elevated; posterior angles weakly produced (fig. 16); marginal stria complete; surface with dense punctures on anterior part, sparser on rest, disc almost smooth; shallow impression near base of second dorsal stria. Elytra with sides parallel; weakly convex; first dorsal stria complete, second and third reaching middle; outer subhumeral stria complete; marginal and outer subhumeral striae united medially; epipleurae irregularly punctate, with deep elongate median impression, without striae; elytra finely and sparsely punctulate, mixed with coarse setigerous punctures.

Propygidium with dense setigerous punctures. Pygidium with smaller and less dense punctures.

Prosternal lobe and keel at approximately the same level, rugose; inner prosternal striae well impressed, with two projections on apical 2/3 (fig. 43), then evanescent, outer prosternal striae well impressed. Meso-metasternal excavation deep; mesosternum with narrow and deep lateral foveae. Metasternum more finely punctate on disc; inner lateral stria short, only reaching middle; outer striae long, not reaching metacoxae; sides with coarse, irregular and dense punctures.

First abdominal sternite finely punctulate.

Legs stout and very expanded, with microsetae and macrosetae.

Aedeagus with the common morphology.

Length 1.7-1.9 mm. Width 1.4-1.5 mm.

Type material

The holotypes of *Hoeterius punctulatus* Lucas (1) and *Hetaerius lioderus* Fairmaire (2) have been studied [both in MNHN] and are labelled as follows: (1) /Berrouaghia/, /*punctulatus* Luc., Coll. Ancey/, /Type/, /Ex. retrouvé dans la Coll. Ancey v. notes Bedel, Dr. Auzat/, /Coll. Dr. V; Auzat (c.v.)/, /*Sternocoelis punctulatus* Luc./; (2) /Pic ?/, /*S. lioderus* Fair., Coll. Bonnaire/, /Coll. Dr. V. Auzat/, /*Sternocoelis punctulatus* Luc./.

Two specimens of the type series of *Hetaerius cavisternus* Marseul have been examined [all in MNHN]. The lectotype and one paralectotype are now designated. LECTOTYPE labelled: /*Hetaerius cavisternus*, Constantine/, /Tipus de Marseul/. PARALECTOTYPE labelled: /*Hetaerius cavisternus*/, /*Hetaerius cavisternus punctulatus*, Alger, Lewis/, /Muséum Paris, Coll. de Marseul, 1890/.

Other material examined

Seven specimens of the DEI: (1) /T. el Had, 1.5.92/, /Coll. Kraatz/, /Bickhardt det./, /*S. punctulatus* Lucas/; (2, 3, 4 and 5) /Berrouaghia, Alger, Ancey/, /*punctulatus* Luc./, /Coll. L. v.

Heyden, DEI Eberswalde/; (6) /Dra el Mizan/, /Ancey/, /Coll. L. v. Heyden, DEI Eberswalde/; (7) /Kabylia, Ancey/, /Coll. L. v. Heyden, DEI Eberswalde/.

Four specimens of the MHNG: (1) /T. el Had/, /*Sternocoelis punctulatus* Lew./; (2 and 3) /Teniet el Had/, /*Lioderus Fairm.*/, /*punctulatus brevisternus*, *Lioderus*/; (4) /*pluristriatus*, *Daya*/.

Twenty-one specimens of the MNHN: (1) /Boghari, 6.3.1914/, /Muséum Paris, ex Coll. P. de Peyerimhoff/; (2, 3, 4, 5, 6, 7 and 8) /Bou Berak près Dellys, Algérie/, /Coll. Dr. V. Auzat (c.v.)/, /*Sternocoelis punctulatus* Luc./; (9) /Roussel, constatation/; (10) /Teniet el Had, avril/, /*Sternocoelis punctulatus*/; (11) /Boghari, Ancey/, /Muséum Paris, 1933, Coll. Desbordes/, /*punctulatus* (Coll. Bickhardt)/; (12 and 13) /Bône, abr. 93/, /*cavisternus*/; (14) /Bonalem, Berrouaghia, 27.4.1934/, /*Sternocoelis punctulatus* Lucas/; (15) /Teniet/, /*Sternocoelis punctulatus* Luc., Lewis 99/, /Teniet el Had/; (16) /T. el Aid, 2.5.92/, /*punctulatus* Lucas/; (17) /Zuauia des Mouzaïna, 29 mai 1919/; (18) /Medeah/, /Typiques Théry/; (19) /Tiaret, dépt. d'Oran, de Vauloger/; (20) /Garn el Kef, Mouzaïre, Mai 1906/, /*Sternocoelis punctulatus* Lucas/; (21) /Lalac, 19 mai 1907/, /*Sternocoelis punctulatus* Lucas/.

Five specimens of the MNHU labelled: (1) /Algier/, /Coll. J. Schmidt/, /Zool. Mus. Berlin/; (2) /Teniet el H., Bedel, IV.81/, /*lioderus Fairm.*/, /Zool. Mus. Berlin/; (3, 4 and 5) /Teniet Had, 1.5.92/, /*punctulatus* Lucas/, /Zool. Mus. Berlin/.

Two specimens of the TM labelled: /Bou Berak, près Dellys, Algérie/, /*Sternoc. punctulatus* Luc., Coll. Reitter/.

Sixteen specimens of the TY all labelled /Bou Berak, près Dellys, 6-11 Mai 1901, Dr. A. Chobaut/, /*punctulatus*/.

Distribution

S. punctulatus is very common in the northern Algeria.

Ecology

This species were collected in winter and spring at middle altitudes. They inhabits nests of *Aphaenogaster* sp. and *Messor barbarus*.

Sternocoelis atlantis Théry, 1921

(Figs 17, 44 and 62)

Sternocoelis atlantis Théry, 1921: 17.

RE-DESCRIPTION

Colour light brown, shiny; body rather convex; covered with two types of dense setae.

Frons very rugose, with dense long setae; frontal stria cariniform, irregular, evanescent on epistoma; labrum slightly concave, truncate; mandibles large, convex, rugosely punctate and covered with dense microsetae; antennal scape very enlarged, surface rugose and microsetose.

Pronotum weakly convex; anterior angles truncate and elevated, posterior very produced (fig. 17); sides subparallel, with marginal stria complete; surface covered with dense setigerous punctures, almost rugose near anterior angles; with a deep depression near base second dorsal stria. Elytra wide and convex; first dorsal stria complete, second fine, not reaching middle; outer subhumeral stria complete, joined to marginal stria beyond middle; epipleurae without striae.

Propygidium setose, with coarse and dense setigerous punctures. Pygidium less densely punctate.

Prosternum finely rugose and with mid-length setae; lobe more prominent than keel and slightly emarginate (fig. 44); keel medially slightly concave, with obsolete inner prosternal striae, at same level as outer prosternal striae; outer prosternal striae more impressed than the inner. Meso-metasternal excavation deep; mesosternum with deep lateral foveae.

Metasternum with two very oblique lateral striae, well impressed, almost reaching metacoxae, inner stria lacking. Metasternum with dense setigerous granules and dense mid-length setae.

First abdominal sternite with dense setigerous granules and setae. Legs long, punctured, with mid-length setae; protibiae weakly expanded; meso- and metatibiae of similar length as elytra, slightly expanded medially (width similar 1/4 length) (fig. 62).

Aedeagus with the common morphology.

Length 1.7-1.8 mm. Width 1.4-1.5 mm.

Type material

The original description was based on a single specimen.

Holotype in the MNHN (accompanied by an ant) labelled: */atlantis*, Type, Théry/, /Ain Leuh, 112/, /Type/.

Other material examined

One specimen in the MNCN: */atlantis*, Théry/, /Azrou, Maroc, Coll. Théry/, /Co-type/, /M.N.C.N. Madrid/.

There are three specimens in the MNHN (accompanied by ants) labelled as follows: (1) /Azrou, Maroc, Coll. Théry/, /Muséum Paris, 1933, Coll. Desbordes/, */Sternocoelis atlasicus*, Théry, (et sa fourmi)/; (2) /Azrou, Maroc, Coll. Théry/, /Coll. Dr. V. Auzat/, */Sternocoelis atlasicus* Théry, Théry det./; (3) /Azrou, Maroc, Coll. Théry/, /Coll. Dr. V. Auzat/.

Distribution

S. atlantis is only known from the Azrou region in the Moyen-Atlas, Morocco.

Ecology

This species inhabits nests of several species of *Aphaenogaster* in mountainous areas.

Sternocoelis setulosus (Reitter, 1872)

(Figs 18, 45, 63 and 79)

Hetaerius setulosus Reitter, 1872: 179.

Hetaerius bonnairei Schmidt, 1888: 236 (nov. syn.).

Sternocoelis setulosus (Reitter): Lewis, 1888a: 149.

Sternocoelis walkeri Lewis, 1888a: 149 (nov. syn.).

Sternocoelis fulvus Lewis, 1888a: 150 (nov. syn.).

Sternocoelis bonnairei (Schmidt): Lewis, 1888a: 154.

RE-DESCRIPTION

Colour reddish brown, shiny; body weakly convex; covered by very long and erect setae and other microsetae.

Frons weakly rugose; frontal stria cariniform, evanescent on epistoma; labrum short, flat, with sparse microsetae; mandibles large, punctate and microsetose; antennal scape very enlarged, rugose and setose.

Pronotum weakly convex; anterior angles truncate, slightly elevated, and slightly produced posteriorly; sides not parallel (fig. 18); marginal stria complete; surface with small punctures mixed with other coarse setigerous punctures, denser on sides and base; anterior depression near base of second dorsal stria. Elytra densely punctate and with other setigerous punctures, almost rugose; first dorsal stria complete, second reaching middle and third shorter; outer subhumeral stria complete, joined medially to marginal stria; epipleurae somewhat rugose, without striae.

Propygidium and pygidium with dense setigerous punctures.

Prosternum with lobe and keel at slightly different levels and separated by a shallow depression (fig. 45); lobe rugose and bisinuate; keel with distinct outer stria, and inner striae fine, approaching; surface between both striae slightly punctate and microsetose; prosternal keel long. Meso-metasternal excavation deep; mesosternum setose, with deep lateral foveae. Metasternum setose, finely punctulate on disc; lateral striae well impressed, inner complete, not oblique, medial complete and oblique, and outer short; sides fossulate.

First abdominal sternite finely punctulate and microsetose.

Legs densely setose, long, weakly expanded; meso- and metacoxae medially slightly expanded (fig. 63).

Aedeagus as figure 79.

Length 1.4-1.6 mm. Width 1.0-1.3 mm.

Type material

The holotype of *Hetaerius setulosus* Reitter [in TM] has been studied, it is labelled: /Holotypus, *Hetaerius setulosus*, Reitter 1872/, /setulosus Typ., Oran Leder/, /Abd el Kader, Oran Leder/, /Coll. Reitter/.

Four specimens of the type series of *Hetaerius bonnairei* Schmidt have been examined. The lectotype and three paralectotypes are now designated. LECTOTYPE ♀ labelled: /Type/, /Edough/, /Coll. J. Schmidt/, /Zool. Mus. Berlin/, /Bonnairei Schmidt/ [in MNHU]. PARALECTOTYPES: one ♀ labelled as the lectotype, in the same Museum; one ♀ labelled /Edough, Coll. Bonnaire/, /Edough/, /Type/, /Coll. Dr. V. Auzat/, /*Sternocoelis Bonnairei* Schm./ and one ♂ with the same labels and moreover /L'étiquette écrite de la main de Schmidt a été enlevée?? Pourquoi??, Dr. Auzat/ [both in MNHN].

Five specimens of the type series of *Sternocoelis walkeri* Lewis have been examined. The lectotype and four paralectotypes are now designated. LECTOTYPE labelled: /Type/, /Maison Carrée/, /*Sternocoelis walkeri* Lewis, Type/, /8.3.84/, /G. Lewis Coll., B.M. 1926-369/ [in NHML]. PARALECTOTYPES [the three first specimens in NHML and the fourth in MNHU] labelled: (1) /Mahadid, Algeria/ and the same last label; (2) /Dj. Mahadid, E. Simon/ and the same last label; (3) /8.3.84/, /Walker/ and the same last label; (4) /Type/, /Alger, Lewis/, /*Hetaerius walkeri*, Type Lewis/, /Zool. Mus. Berlin/.

Twenty-eight specimens of the type series of *Sternocoelis fulvus* Lewis have been examined. The lectotype and paralectotypes are now designated. LECTOTYPE labelled: /Type/, /H. Rirha, Algeria, Lewis/, /G. Lewis Coll., B.M. 1926-369/ [in NHML]. PARALECTOTYPES, one specimen of the MNHN labelled /Hamman Rirha (Lewis)/, /Type/, /Coll. Bonnaire/, /*Sternocoelis fulvus* Lewis/, /Coll. Dr. V. Auzat/, /*Sternocoelis fulvus* Lewis/, the remaining specimens are deposited in the NHML and labelled as follows: eighteen specimens like the lectotype; two specimens /Hamman Rirha (Lewis), 23.2.88/, /G. Lewis Coll., B.M. 1926-369/;

five specimens /Hamman Rirha, 17.4.94/, */fulvus/* and the same last label: one specimen /Hamman Rirha, 26.2.88/, /Algeria/, /Fry Coll. 1905/, */Sternocoelis fulvus* Lew./.

Other material examined

Ten specimens of the DEI labelled as follows: (1, 2 and 3) /Cirta, Lewis, 1894/, /Coll. Kraatz/, */Sternocoelis bonnairei* Sch./, /Bickhardt det./; (4 and 5) /Blidah, Algier/, */Sternocoelis fulvus* Lew./ and the same two last labels; (6 and 7) /Oran/ and the same two last labels; (8, 9 and 10) /Hamman Rirha, Lewis, 1888/, */Sternocoelis bonnairei* Lew./.

Fourteen specimens of the MHNG labelled as follows: (1, 2 and 3) */Sternocoelis setulosus* Reitt./, /Bou Berak près Dellys, Algérie/; (4 and 5) /Bou Berak, Kabilie, L. Puel/, */E. setulosus/*; (6 and 7) /Thlemcen/, /Daya/, */setulosus/*; (8) /Termi, 9.IV/, */Sternocoelis setulosus* Rtt. bei *Aph. testaceopilosa/*, /Coll. A. Forel/; (9 and 10) /Bougie (Puel)/; (11 and 12) /Algérie: Gde Kabylie, 9 km E Yakouren, 930 m, 13.V.1988, Besuchet, Löbl, Burkh./, */Sternocoelis* sp. 2, det. S. Mazur/; (13 and 14) /Tunisie, Belig. près Cap Negro, 5.IV.62, Cl. Besuchet/, */Sternocoelis* sp., det. S. Mazur/.

Fifty-two specimens of the MNHN labelled as follows: (1) /Hamman Rirha/, */fulvus/*, /Coll. Dr. V. Auzat/, */Sternocoelis fulvus* Lewis/; (2) /Souk-Ahras, 16-4-92/, /Muséum Paris, 1933, Coll. Desbordes/, */Bonnairei*, Coll. Bickhardt 88/; (3) /Medjez Amar, Algérie, L. Clouet des Pesrouches/, */Sternocoelis bonnairei* Coll. Théry/; (4 and 5) /Hamman Rirha/, */St. fulvus* Lew., Lewis 99/; (6) /Tisourda, 11 juin 1916/; (7) /Babor (Sad.), 12 juin 1912/; (8) */Sternocoelis setulosus*, Juin 88/, /Reitter, Dayet/, /Muséum Paris, Coll. de Marseul, 1890/; (9) /Blida (Algérie), L. Bleuse/, */Sternocoelis setulosus* Reitter/; (10-13) /Bou Berak près Dellys, Algérie/, /Coll. V. Auzat/, */Sternocoelis Bonnairei* Schm./; (14) /Mt. Babor, Algérie, Coll. Théry, *Sternocoelis setulosus/*; (15) /St. Charles, SO du lac, 21 Mars 1894/, */St. Bonnairei* Schmidt/; (16) /Coll. Théry/, /Bugeaud, L. Clouet des Pesrouches, Medjez Amar, Algérie/, /Coll. V. Auzat/, */Sternocoelis Bonnairei* Schm./; (17) /El Milia, avril 1901, de Vauloger/, */Sternocoelis Bonnairei* Schm./; (18) /Tlemcen, Coll. Bonnaire/, */Sternocoelis setulosus/*; (19) /Saïda, Coll. Bonnaire/, */Sternocoelis setulosus* Rtt./; (20) /Ravin de St. André de Mers-el-Kébir, 12-XII-59, J. Barbier/, /Dans fourmilière d'*Aphaenogaster testaceopilosa/*, */Sternocoelis setulosus* Rtt./; (21-25) /Daya, Coll. Grouvelle/, /Coll. Dr. V. Auzat/, */Sternocoelis setulosus* Rtt./; (26-32) /Dj. Babor, 5.1901, Dr. Vauloger/, */Sternocoelis walkeri* Lew./; (33-46) /Dj. Babor, 5.1901, A. Vauloger, Théry/; (47) /Tienet el Had, de Vauloger/; (48) /Mt. Edough, Algérie, A. Théry/, */Bonnairei/*; (49) /Col des Oliviers, Algérie/, /Coll. Théry/; (50) /Oued Cher, L. Clouet des Pesrouches à Medjez Amar, Algérie/; (51-52) /Algeria, Lewis/, /Muséum Paris, 1933, Coll. Desbordes/, */Sternocoelis fulvus* Lewis/.

Thirteen specimens of the MNHU labelled as follows: (1) /Oran, Lewis, 22.3.88/, /compared with Type, 8.6.88/, */Hetaerius setulosus* Reitter/, /Zool. Mus. Berlin/ (all the specimens with the same last label); (2) /Oran/; (3) /Daya, Bedel/, /Coll. J. Schmidt/, */setulosus* Reitter/; (4 and 5) /Algier, Desbr./; (6) /Hamman/; (7) /Tienet el H., Bedel/; (8) /Cirta, 2.5.94/, */S. bonnairei* Sch./; (9) /Medjez Amar, Algérie, L. Clouet des Pesrouches/; (10) /Souk-Ahras, 10.4.92/, */S. bonnairei* Sch. ??/; (11) /Constantine, G. Lewis, 19.3.92/; (12) /Bone, 1.4.92/, */S. bonnairei* Schm./; (13) /Hamman Rirha, 1888/, */Hetaerius fulvus* Lewis/.

Twenty-four specimens of the NHML labelled as follows: (1-5) /Blida, Lewis, 19.3.91/, /G. Lewis Coll., B.M. 1926-369/ (all the specimens whis this label); (6 and 7) /Blida, 29.4.92/, */S. fulvus* Lewis/; (8-15) /Blida, 28.4.94/; (16) /Blida Forest, 4.5.92/, */Walker/*; (17) /Blida, 19.3.91/; (18) /Bone, 1.4.92/, */S. Bonnairei* Sch./; (19-21) /Bône/, */Sternocoelis pectoralis/*; (22-24) /Mt. Babor, Algérie, Coll. Théry/.

Three specimens of the NHMW labelled as follows: (1 and 2) /Medjez Amar, Algérie, L. Clouet des Pesrouches/, */Sternocoelis Bonnairei* Schm./; (3) /Bou Berak, Kabylie, L. Puel/, */comosellus*, det. J. Müller/.

Fourteen specimens of the TM and labelled: (1) /Col des Oliviers, 17.3.1894/, */Sternocoelis punctulatus* Lewis, Coll. Reitter/; (2) /St. Charles, SO du lac, 21 Mars 1894/, */Sternocoelis punctulatus* Lewis, Coll. Reitter/; (3, 4 and 5) /Chanzy 1890, de Vauloger/, */Sternoc. setulosus* Reitt., Coll. Reitter/; (6, 7 and 8) /Medjez Amar, Algérie, L. Clouet des Pesrouches/, */Sternoc. Bonnairei* Schm., Coll. Reitter/; (9, 10, 11 and 12) /Hamman Rirha,

Algeria/, */Sternoc. fulvus* Lewis, Coll. Reitter/; (13 and 14) /Algeria/, */Sternocoelis setulosus* Reitt., det. J. Frivaldszky/, */setulosus* Rtt., det. Théron/.

Thirty-five specimens in the TY, from 31 of them were labelled /Bou Berak près Dellys, Algérie/, */Sternocoelis setulosus/* and other four specimens labelled /Bougie, L. Coutazar/.

Distribution

S. setulosus ranges throughout northern Algeria and Tunisia.

Ecology

This species exists in mountainous areas and is active in winter and spring. It inhabits nests of *Aphaenogaster depilis* Santschi and *A. afra* Santschi.

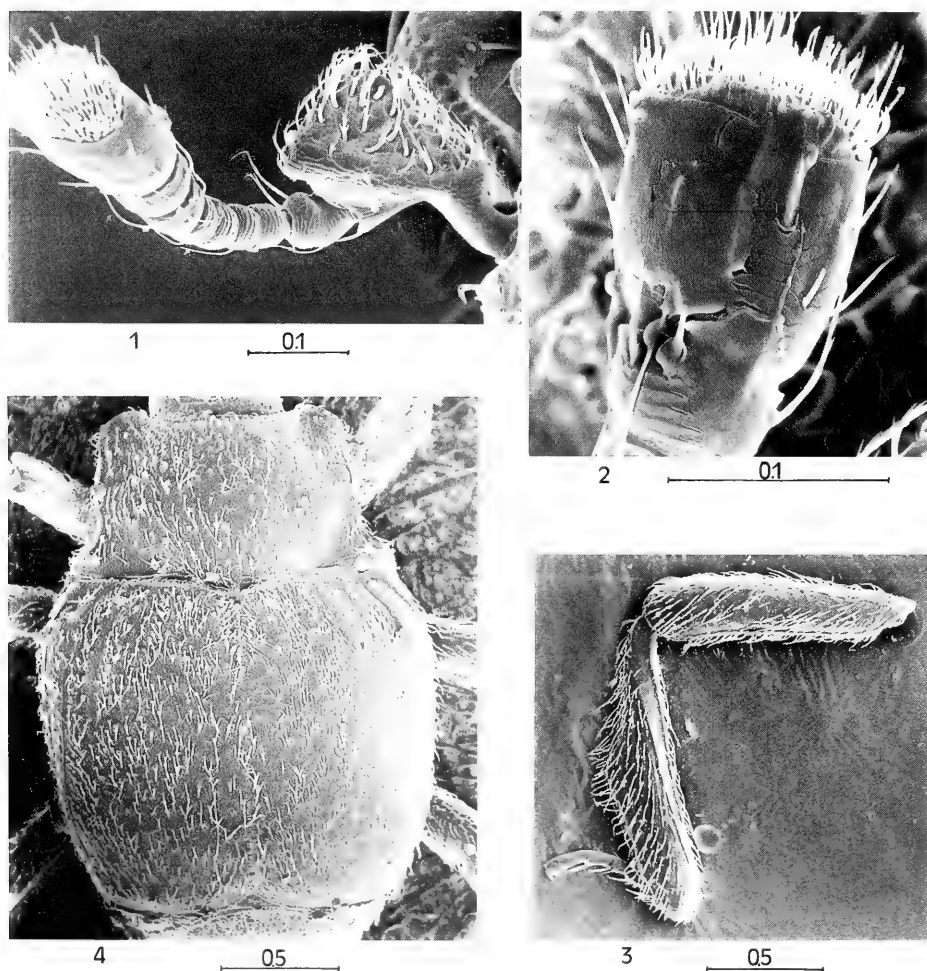


FIG. 87

Sternocoelis hispanus (Rosenhauer) - 1. Left antenna in dorsal view; 2. Antennal club in dorsal view; 3. Outer side of midleg; 4. Upper side of body. Scale in mm.

***Sternocoelis hispanus* (Rosenhauer, 1856)**

(Figs 19, 46, 64, 80 and 87)

Hetaerius hispanus Rosenhauer, 1856: 89.*Sternocoelis hispanus* (Rosenhauser): Lewis, 1888a: 148.*Haeterius incisus* var. *gili* Escalera, 1929: 376 (synonymized by Yélamos, 1993: 160).**RE-DESCRIPTION**

Colour light brown, shiny; body weakly convex; covered with two types of yellow setae, one long and erect, and the other shorter (fig. 87, 4).

Frons rugose; frontal stria cariniform and irregular, evanescent on epistoma; labrum flat and truncate; mandibles large, with dense setae; antennal scape enlarged (fig. 87, 1 and 2).

Pronotum convex, with anterior angles slightly elevated; posterior angles very produced (fig. 19), with shallow anterior impression near base of second dorsal stria; sides parallel, with marginal stria interrupted next to anterior angles; surface with setigerous pores, larger and denser on apical end. Elytra strongly expanded, convex; covered with indistinct microscopic puncticles, and irregular setigerous pores and granules; first dorsal stria complete, second apically shortened and third reaching middle; outer subhumeral stria surpassing middle and marginal stria strong and complete; epipleurae rugose, without striae.

Propygidium and pygidium with dense setigerous pores.

Prosternum rugose and setose; keel broad and flat, except near lobe, where there is a wide depression, as well as on base; base slightly sloped toward mesosternum (fig. 46); inner striae weakly prominent, subparallel; prosternal lobe deflexed; outer striae short and fine. Meso-metasternal excavation very deep; mesosternum with short and dense setae; sides fossulate. Metasternum long and pubescent, with granules and punctures on disc; sides fossulate; lateral striae obsolete, only distinct two oblique striae, reaching middle.

First abdominal sternite with setigerous pores; sides with coarse punctures.

Legs very long; femora and tibiae of same length; proportion between metatibia and body length 0.56-0.58; protibiae slightly expanded at apical half; mesotibiae medially strongly expanded (fig. 87, 3); metatibiae expanded at apical part, nearly 1/4 total length metatibia (fig. 64); densely setose and slightly rugose.

Aedeagus as figure 80.

Length 1.5-2.1 mm. Width 1.2-1.7 mm.

Type material

Two specimens of the type series of *Hetaerius hispanus* Rosenhauer have been examined, deposited in the DEI, being now designated as lectotype and paralectotype. The remaining specimens in the St. Petersburg Zoological Institute were unavailable for study. They should be considered paralectotypes. LECTOTYPE labelled: */hispanus*, S. de Ronda, Andalus (Rosh.), bei *Aphenogaster senilis* Mayr./, /Coll. L. v. Heyden, DEI Eberswalde/, /Syntypus/. PARALECTOTYPE labelled: */Andalus*, Rosenhr./, /Coll. L. v. Heyden, DEI Eberswalde/.

The lectotype and nine paralectotypes of *Haeterius incisus* var. *gili* Escalera have been examined [all in MNCN]. Lectotype ♀ labelled: */Candeleda*, 30.3.1929/, */St. incisus* var. *gili* Esc./, Paralectotypes: 4 ♀♀ and 4 ♂♂ labelled like the lectotype; a ♀ */Dehesa Rincón*, Candeleda, 30.3.1929/.

Other material examined

Nine specimens of the DEI labelled as follows: (1) /Alhambra/, /Coll. Kraatz/, /Bickhardt det./, /*Sternocoelis hispanus*/; (2 and 3) /Escorial, Lewis, 28.4.88/, moreover the second and the third labels; (4 and 5) /Madrid/, moreover the second and the third labels; (6) /Cordoba/, moreover the second and the third labels; (7 and 8) /*Haeterius hispanicus*/, /Portugal/, /Coll. Stierlin/; (9) /Hispanus, Hispania, Merkl/, /*Aphaenog. testaceopil.*/, /Coll. L. v. Heyden, DEI Eberswalde/.

Four specimens of the EEZA labelled: /Nava de S. Pedro, S. Cazorla, Jaén, A. Cobos leg./, /V. 1962/.

Ten specimens of the MHNG labelled as follows: (1-9) /Maroc-Rif, Bab Besen, près Mt. Tidiguin, (1150 m) 23.IV.60, Cl. Besuchet/, /*Sternocoelis* sp., det. S. Mazur/; (10) /*hispanicus*, Cintra, Lewis/.

Thirty specimens of the MNCN labelled as follows: (1-9) /Tizi Taka, Beni Seddat, Rif, VI-1930, Exp. C. Bolivar/; (10-13) /Imasinen, Beni Seddat, Rif, VI-1930, Exp. C. Bolivar/; (14-20) /Iguermalen, Beni Mesdui, VI-1932, M. Escalera/; (21) /Iguermalen, Targuist, Rif, VI-1930, Exp. C. Bolivar/; (22) /Zoco Telata, Ketama, Rif, VI-1930, Exp. C. Bolivar/; (23-28) /Bab Chiquer, Ketama, Rif, VI-1932, M. Escalera/; (29-30) /Candeleda, 30.3.1929/.

Thirty-one specimens of the MNHN labelled as follows: (1-3) /Cintra, 12-4-86/, /*Sternocoelis hispanicus*/; (4) /Andalousie/; (5-6) /Alcala, 3-92/, /*Sternocoelis hispanicus* Rosh./; (7) /Montarco (Madrid)/, /Coll. Dr. V. Auzat/, /*Sternocoelis hispanus* Rosh./; (8) /Madrid, ex Escalera/ and the same two last labels; (9) /Escorial, Lewis, 28.4.88/, /Coll. Bonnaire/ and the two last labels; (10) /Lusitania merid., Coll. Bonnaire/ and the two last labels; (11) /Pozuelo, de la Fuente/ and the two last labels; (12) /Alcala 91, Martinez/, /*Hetaerius hispanus*/, /SAMML Dr. Daniel/ and the same last labels; (13) /Alcala, Andalousie/, /*hispanus* Rosh./; (14) /Pozuelo de Calatrava (Espagne)/, /*St. hispanus*/; (15) /Cintra, Lewis/; (16) /Candeleda, 20-3-1929/, /*S. hispanus* Rosh./; (17) /*Hetaerius hispanus*, mars 22.91, Lewis 88/, /Madrid, 22-3-54/, /Muséum Paris, Coll. de Marseul, 2842-90/; (18-19) /Cintra, Lewis, 8-4-86/, /Muséum Paris, Coll. de Marseul, 2842-90/; (21-22) /Cintra, Lewis, april 84/, /*Hetaerius hispanus*, Cintra, 1.4.86, Lewis 86/; (23-28) /Muséum Paris, Coll. de Marseul, 2842-90/, /*Hetaerius hispanicus* R. Cintra (Lewis) 1886/; (29) *Hetaerius hispanicus*, Tanger, Juin 81/, /Muséum Paris, Coll. de Marseul, 1890/, /Tanger/, /Coll. Camille Van Volxem/; (30) /Cintra, Coll. Bickhardt/, /Muséum Paris, 1933, Coll. Desbordes/, /*hispanus*/; (31) /Madrid, Lewis/, /*Sternocoelis hispanicus*/ and the same last label.

Six specimens in the NHMW labelled as follows: (1) /*hispanus* Rosh., Madrid, Bauduer/, /c. Epplsh. Steind. d./, /*hispanus*/; (2) /Lusitan. Reitter 1888/; (3) /Lusitania/, /collection Kaufmann/, /*Sternocoelis hispanus*, det. J. Müller/; (4) /Sartorius 1876/; (5) /Hispania/, /*hispanus* Ros./; (6) /*Sternocoelis hispanus*/.

Five specimens of the TM labelled as follows: (1-2) /Lusitania/, /Cintra, Lewis, 3.4.86, Lusitania/, /*Sternoc. hispanus*, Rosenh., Coll. Reitter/; (3) /Hispania, Madrid/, /*Sternoc. hispanus*, Rosenh., Coll. Reitter/; (4-5) /Portugal Merid./, /*Hetaerius hispanus*, det. J. Frivaldsky/, /*hispanus* Rosh., det. Théron/.

Fourteen specimens of the TY labelled as follows: (1-3) /Villapalacios, (Albacete), 21.4.84, T. Yélamos leg./; (4-5) /Pto. Pocos, Albacete, 21.4.84, T. Yélamos leg./; (6) /Provinz, Madrid/, /Hispania, Reitter/; (7) /Cintra, (Lewis) 1886/, /*Hetaerius hispanicus*/; (8) /*Heterius hispanus*, Madrid/; (9-13) /Cand., 9.4/; (14) /Candeleda, 20.4.1930/.

Distribution

S. hispanus occurs in central and southern Portugal and Spain, as well as in the Rif region in the north of Morocco.

Ecology

This species is the most common *Sternocoelis* in the Iberian Peninsula. It inhabits nests of *Aphaenogaster senilis* Mayr. It lives at low and middle altitudes.

Sternocoelis arachnoides (Fairmaire, 1877) (Figs 20, 27, 47, 55, 65, 81 and 88)

Hetaerius arachnoides Fairmaire, 1877: 98.

Sternocoelis arachnoides (Fairmaire): Lewis, 1888a: 150.

Sternocoelis araneoides (Fairmaire): Kryzhanovskij & Reichardt, 1976: 410 (*lapsus calami*).

RE-DESCRIPTION

Colour light brown, shiny; body convex; sparsely covered with very long, yellow setae. Habitus as figure 88.

Frons rugose and setose; frontal stria cariniform, irregular and finer on epistoma; labrum short and truncate; mandibles large, with dense microsetae; antennal scape very large and microsetose.

Pronotum narrow and weakly convex; anterior angles produced, slightly elevated; posterior angles strongly produced (fig. 20); sides bisinuate, subparallel, with marginal stria interrupted near anterior angles; apical third covered with punctures and setigerous granules, sparser on rest, smooth; shallow depression near base third dorsal stria. Elytra weakly convex, subparallel, with coarse and sparse setigerous punctures; first dorsal stria complete, second and third basal; outer subhumeral stria well impressed, complete, joined to marginal stria medially; epipleurae slightly rugose, microsetose, with a long irregular stria (fig. 27).

Propygidium and pygidium sparsely covered with setigerous pores of different sizes.

Prosternum rugose and setose; keel convex over its entire length, basally sloping towards mesosternum and apically towards prosternal lobe; inner striae strong, slightly prominent, outer striae slightly impressed; prosternal lobe bisinuate, weakly produced and separated from keel by a shallow and wide depression (fig. 47). Mesometasternal excavation very deep; mesosternum with oblique deep depressions near to mesocoxae, extended through deep foveae internally. Metasternum elongate, with nearly smooth surface; sides covered with dense microsetae; dorsal striae fine, of similar length and just surpassing mesocoxae.

First abdominal sternite with dense setigerous pores and microsetae on disc, denser on sides.

Legs very long (fig. 65), with femora and tibiae of same length (proportion between length metatibia and total length body 0.73-0.75); tibiae somewhat expanded, densely setose.

Aedeagus as figure 81.

Length 1.5-1.6 mm. Width 1.1-1.2 mm.

Material examined

The type series was not found in the Fairmaire collection (MNHN).

Eight specimens were seen of the DEI with the following labels: (1-2) /Tanger, Rolph/, /Peyerimhoff det./, /*Sternocoelis arachnoides* Fairm./; (3-4) /Tanger, Lewis/, /Coll. Kraatz/, /Bickhardt det./; (5) /Marocco, Coll. O. Leonhard/, /Coll. Leonhard/, /*Hetaerius arachnoides* Fairm./; (6-7) /Maroc/, /Coll. Stierlin/, /*H. arachnoides* Fairm./; (8) /Tanger, Desbroch./, /*arachnoides* Fairm./, /Coll. L. v. Heyden, DEI Eberswalde/.

Nine specimens of the MHNG: (1) /Maroc/, /*Sternocoelis arachnoides*, 1974, det. S. Mazur/; (2-5) /Maroc, Beccard/ and the same last label; (6-7) /Maroc, Vaucher/ and the same last label; (8) /P. de Borre/, /Maroc/; (9) /*arachnoides*, Frm., Tanger, Janvier/.

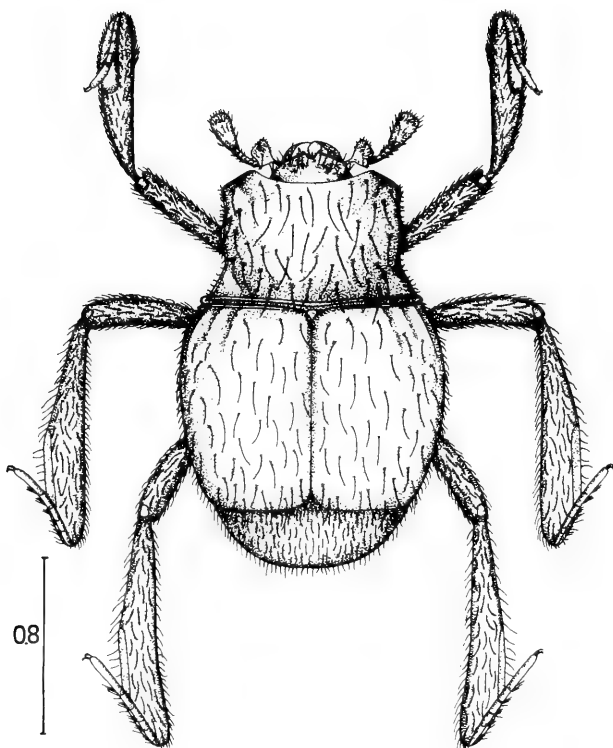


FIG. 88

Dorsal habitus of *Sternocoelis arachnoides* (Fairmaire). Scale in mm.

Five specimens of the MNCN: (1-2) /Larache, M. Escalera/; (3-5) /Larache, 5.1915/.

Twenty-two specimens of the MNHN: (1-3) /Tanger, ex Escalera/, /Coll. Dr. V. Auzat/, /*Sternocoelis Arachnoides* (Fair.)/; (4-5) /Tangier, Lewis, 2.4.88/, /Coll. Bonnaire/ and the same two last labels; (6-7) /Larache (Maroc), Escalera/ and the same two last labels; (8) /Maroc, H. Vaucher/, /Collection E. de St. Albin/, /*Sternoscoelis arachnoides* Fairm./; (9) /1907, Tanger/, /Maroc, ex Musaeo, H. Vaucher, 1908/, /*Hetaerius arachnoides* Frm./; (10) /Maroc, Olcese/; (11) /Andalousie/; (12) /4.95, Tanger/; (13) /Tangier, Lewis, 2.4.88/; (14-17) /Tangier, Lewis, 7-4-88/, /*Sternocoelis arachnoides* Lew. 88/, /Muséum Paris, Coll. de Marseul, 1890/; (18-20) /Maroc, E. Tisson/, /*arachnoides* (Peyer. det. 1909)/ and the same last label; (21) /Morocco,

Lewis/, /Muséum Paris 1933, Coll. Desbordes/, /*Sternocoelis arachnoides*/; (22) /Coll. Fleutiaux/, /*arachnoides*/, /Muséum Paris 1933, coll. Desbordes/.

Three specimens of the NHMW: (1) /3.96, Tanger/, /Collect. Hauser/, /*H. arachnoides* Frm./; (2-3) /Tanger, Herrmann/.

Four specimens of the TM: (1-2) /Tangier, Lewis/, /*Sternoc. arachnoides* Fairm., Coll. Reitter/; (3-4) /Marokko, Tanger/, /*Sternoc. arachnoides* Fairm., Coll. Reitter/.

Four specimens of the TY: (1-4) /Tanger, 4.1904/, /Tanger, Lewis/, /*Sternocoelis arachnoides* Fairm/.

Distribution

S. arachnoides occurs mainly in the northern Morocco (Tangier and Larache), but there are several specimens labelled "Andalusia" and "Spain", without precise localities.

Ecology

This species inhabits nests of *Aphaenogaster sardoa* Mayr and *A. strioloides* Forel and is active in winter and spring. It occurs at lower elevations.

Sternocoelis slaoui Théry, 1921

(Figs 21, 48, 56 and 66)

Sternocoelis slaoui Théry, 1921: 18.

Sternocoelis cancriformis Escalera, 1921: 126 (syn. nov.).

RE-DESCRIPTION

Colour reddish brown, shiny; body weakly convex, broadly oval; with long yellow, setae and microsetae.

Frons with scarce setigerous pores; frontal stria cariniform, irregular and evanescent on epistoma; labrum flat, truncate; mandibles large, convex and setose; antennal scape very enlarged and setose.

Pronotum wide and weakly convex; anterior angles expanded, slightly elevated; posterior angles weakly produced (fig. 21); sides of pronotum with marginal stria interrupted near posterior angles; surface covered with setigerous granules; base of pronotum with deep depression near base of third dorsal stria. Elytra weakly convex; sides subparallel and with sparse setigerous granules and pores; dorsal striae fine, very curved outward, first complete, second reaching middle and third basal; outer subhumeral stria complete, not united to marginal stria, only reaching middle; epipleurae rugose and without striae.

Propygidium and pygidium with sparse, coarse setigerous pores.

Prosternum with keel longitudinally convex over its entire length; base sloping toward mesosternum; also sloping apically within a wide depression between lobe and keel (fig. 48); inner prosternal striae divergent, somewhat prominent, with surface between them nearly smooth and with setae on anterior end; outer prosternal striae well impressed; prosternal lobe rugose and deflexed. Meso-metasternal excavation very deep; mesosternum almost vertical, with deep impression on both sides near to mesocoxae, and deep foveae inside body. Metasternum long, finely punctulate on

disc, sides with coarse setigerous punctures; inner lateral stria well impressed and nearly complete, medial stria less impressed and somewhat shorter; outer stria very fine and short.

First abdominal sternite with disc convex and setigerous granules.

Legs very long (figs 56 and 66), with femora and tibiae of same length (length metatibia/total length body = 0.63-0.65); tibiae slightly expanded, punctate and setose.

Aedeagus like *S. arachnoides*.

Length 1.4-1.5 mm. Width 1.1-1.2 mm.

Type material

The holotype of *Sternocoelis slaoui* Théry [in MNHN] is labelled as follows: /Kil 13, 3-3-1920/, /Route de Salé à Kenitra/, /*Sternocoelis slaoui* Théry/, /Type/ (accompanied by an ant).

The type series of *Sternocoelis cancriformis* Escalera were also seen. The lectotype and ten paralectotypes are now designated. LECTOTYPE ♂ labelled: /Larache, 5.1915/, /sintipo/ [in MNCN]. PARALECTOTYPES, three specimens in MNCN: one ♂ labelled like the lectotype: 2 ♀♀ /Larache, M. Escalera/, /Sintipo/; seven specimens in MNHN: /Larache/, /Paratype/, /*Sternocoelis cancriformis* Esc./; /Larache, M. Escalera/, /*cancriformis*, Cotype, Esc./; /Larache/, /Type/, /Type qui a servi à Escalera pour faire son dessin/, /*Sternocoelis cancriformis*, type Esc./, /Coll. Dr. V. Auzat/ and four specimens labelled /Larache/, /Maroc, ex Escalera/, /Coll. Dr. V. Auzat/, /Paratype/, /*Sternocoelis cancriformis* Es./.

Distribution

S. slaoui is only known from northern Morocco (Larache and Salé).

Ecology

This species occurs at lower elevations and inhabits nests of *Aphaenogaster sardoa* Mayr and *A. strioloides* Forel.

Sternocoelis comosellus (Fairmaire, 1883)

(Figs. 22, 49, 67 and 82)

Hetaerius comosellus Fairmaire, 1883: 42.

Sternocoelis comosellus (Fairmaire): Lewis, 1888a: 148.

RE-DESCRIPTION

Colour reddish brown, shiny; body convex; with long and short yellow setae.

Frons rugose; frontal stria cariniform, weakly prominent; labrum short, flat and truncate; mandibles large, convex, rugose and with long setae; antennal scape very enlarged, rugose and setose.

Pronotum with anterior angles truncate, not elevated, and posterior angles very produced (fig. 22); sides parallel, rounded and without marginal stria; surface slightly convex and with coarse, dense setigerous punctures, mixed with other punctures, mainly on sides and anterior part. Elytra lacking distinct striae; weakly convex and with mixture of coarse and dense setigerous punctures; epipleurae rugose and without striae.

Propygidium and pygidium with dense setigerous punctures.

Prosternum with lobe deeply emarginate, divided into two parts and forming an obtuse angle with keel (fig. 49); prosternal keel wide, with outer and inner striae well impressed, outer stria fine; inner stria basally recurved towards mesosternum and diverging at apical half. Meso-metasternal excavation shallow; mesosternum without lateral foveae, but with fine oblique impression. Metasternum with disc covered with fine and sparse punctures, and short, fine setae; sides with sparse setigerous punctures; inner lateral stria very short; two outer oblique striae and reaching middle.

First abdominal sternite with small, sparse setigerous punctures, and setae.

Legs very long, not expanded, and with long setae (fig. 67).

Aedeagus as figure 82.

Length 1.3-1.5 mm. Width 1.1-1.2 mm.

Type material

The holotype [in MNHN] has been studied, labelled as follows: /Philipv./, /Type/, /Coll. Bonnaire/, /Coll. Dr. V. Auzat/, /*Sternocoelis comosellus* Type Fairm./.

Other material examined

Six specimens of the DEI labelled: (1) /Constantine/, /Coll. Kraatz/, /Bickhardt det./, /*Sternocoelis comosellus* Fairm./; (2) /Medjez Amar, Algérie, L. Clouet des Pesrouches/, /Bickhardt det./; four specimens /2-94/, /Mamar/, /*comosellus*, Algérie, Théry/, /Coll. L. v. Heyden, DEI Eberswalde/.

Two specimens of the MHNG, both bearing the labels /Constantine/, /Walker Lewis/.

Nineteen specimens of the MNHN labelled: (1 and 2) /2.94/, /Mamar/, /Collection A. Grouvelle/, /Coll. Dr. V. Auzat/, /*Sternocoelis comosellus* Frm./; (3, 4 and 5) /Constantine 92, février, Coll. Hénon/, /Coll. Dr. V. Auzat/, /*Sternocoelis comosellus* Frm./; (6) /Constantine/, /Walker Lew./, /Coll. Dr. V. Auzat/, /*Sternocoelis comosellus* Frm./; (7) /*Sternocoelis fulvus* Lew. 88/, /H. Rirha Lewis, 27.2.88/, /Muséum Paris, Coll. de Marseul 1890/, /*Hetaerius comosellus* Fairm./; (8) /Constantine, Coll. Théry/, /Muséum Paris, 1933, Coll. Desbordes/, /*Sternocoelis comosellus*/; (9, 10, 11, 12, 13, 14 and 15) /Medjez-Amar, Algérie, L. Clouet des Pesrouches/; (16) /*comosellus* Frm., A. Théry, 3r.1901, Medjez-Amar, 2.44/, /*Comosellus*, Cortain/; (17) /Dfoman-Cher/; (16) /Dienard, Algérie, Coll. Théry/; (19) /Constantine, Algérie, Coll. Théry/.

Five specimens of the MNHU labelled: three specimens /D. Ouach, Alger/, /Zool. Mus. Berlin/; one specimen /Constantine Alger/, /*Het. comosellus* Fairm./, /Coll. J. Schmidt/, /Zool. Mus. Berlin/, /*comosellus* Fairm./; one specimen /M. Amar/, /*comosellus*/, /Zool. Mus. Berlin/.

Three specimens of the NHMW all were labelled /Medjez-Amar, Algérie, L. Clouet des Pesrouches/, /Coll. Hauser/, /Bonnairei det. J. Müller/, /*Sternocoelis comosellus* Frm./.

Five specimens of the TM: three were labelled /Medjez-Amar Algérie, L. Clouet des Pesrouches/, /*Sternoc. comosellus* Fairm., Coll. Reitter/; one specimen /Algeria/ and the same last label; one specimen /Algier Reitter/, /*Sternocoelis comosellus*, det. J. Frivaldszky/, /J. Thérond det. 1962, *Sternocoelis comosellus* Frm./.

Distribution

S. comosellus is found in Northern Algeria.

Ecology

This species is known to be active in winter and spring at low altitude. It inhabits nests of *Aphaenogaster canescens* Emery.

Sternocoelis espadaleri n. sp.

(Figs 23, 50, 68, 83 and 86)

DIAGNOSIS

This species is similar to the related *S. comosellus* from Algeria. It differs in having a distinct dorsal striae, a marginal elytral and subhumeral striae which are cariniform, oblique lateral mesosternal foveae and deep meso-metasternal excavation.

DESCRIPTION

Colour reddish brown, shiny; body convex; surface sparsely covered with long and short setae.

Frons wide, with dense setigerous punctures; frontal stria cariniform, reaching epistoma; labrum weakly concave and with setigerous punctures; mandibles large, convex and rugose, with long, dense setae; antennal scape strongly enlarged, rugose, densely setose; antennal club very large, pubescent; eyes large.

Pronotum with anterior angles truncate, weakly produced; posterior angles well produced (fig. 23); sides rounded, subparallel, without marginal stria; disc convex with coarse, dense setigerous punctures; sides rugose, with smaller punctures near base; small deep depression near posterior angles. Elytra very expanded, with dense setigerous punctures and short and long setae; sides rugose and more densely setose; dorsal striae very reduced, appearing as shallow impressions, the first stria more impressed, second and third only reaching middle; subhumeral, marginal and epipleural striae irregular and fine; epipleurae without striae, with coarse, dense setigerous punctures and microsculpture.

Propygidium and pygidium densely covered with setigerous punctures and setae.

Prosternal lobe deeply emarginate and deflexed; keel very wide and slightly rugose, with inner striae very separated, parallel (fig. 50), slightly cariniform, reaching apical 2/3, and outer striae well impressed and at a slightly lower level as inner striae; keel base abruptly sloping toward meso-metasternal excavation. Meso-metasternal excavation very deep; mesosternum strongly sloped, smooth, with oblique, shallow lateral foveae. Metasternum long, depressed, sparsely punctate and with scattered short setae; longitudinal metasternal stria convex at base; inner lateral stria almost reaching 2/3 length metasternum; medial stria reaching metacoxae while outer stria only reaching middle; sides with dense, irregular setigerous punctures and short setae.

First abdominal sternite with shallow transverse depression, with sparse setigerous punctures and setae.

Legs very long (fig. 68), not expanded and with dense setigerous punctures and setae; femora with a ventral groove to receive tibiae; tarsal grooves shallow, mainly on meso- and metatibiae.

Eight male abdominal segment finely sclerotized and rather wide and short; spiculum gastrale very long and Y-shaped (fig. 86); aedeagus with basal piece narrow; parameres very long, not parallel, with an apical emargination almost reaching middle (fig. 83). Female not known.

MEASUREMENTS

Total length 1.8 mm	Maximum width 1.3 mm
Profemur length 0.9 mm	Protibia length 0.8 mm
Mesofemur length 1.0 mm	Mesotibia length 1.1 mm
Metafemur length 1.1 mm	Metatibia length 1.2 mm
Maximum length pronotum 0.7 mm	Maximum length elytra 1.1 mm
Maximum width pronotum 1.0 mm	
Minimum width pronotum 0.9 mm	
Maximum width elytra 1.3 mm	
Minimum width elytra 1.1 mm	

Type material

Two specimens have been studied. HOLOTYPE: ♂ labelled /Maroc, 1660 m, Bou el Ghallat, près Aghbala, lg. Espadaler/, /avec *Aphaenogaster baronii* Cagn., sous chêne vert/, with an ant [in MHNG]. PARATYPE: ♀ labelled /Djebel Irhoud, Agadir Maroc, 1800 m, 23-5-86, X. Espadaler leg./, /Bosc de cedres en nid d'*Aphaenogaster baronii*/ [in JM].

Etymology

I have the pleasure to name this species after my friend and Colleague, ants specialist, Dr. Xavier Espadaler, as a tribute to his valuable collaboration.

Distribution

S. espadaleri is only known from Aghbala (east from El-Ksiba), Moyen-Atlas, central Morocco and Djebel Irhoud (near Agadir) South-western Morocco.

Ecology

The holotype was collected in a nest of *Aphaenogaster baronii* Cagniant together with *Thorictus* (Coleoptera, Thorictidae) on May 16, 1984 and the paratype was collected in a nest of the same ant on May 23, 1986.

S. espadaleri was collected in a mesic oak forest on a North-west facing slope at an elevation of 1,600 m, as well as in a cedar's forest at 1,800 m.

SYSTEMATIC RESULTS

After the study of 792 specimens, it has become clear that a great number of synonyms has been created, mainly on account of differences in punctuation and pilosity. These characters show a high individual variability.

Sternocoelis espadaleri is described as a new species and 14 species are dropped into the synonymy of 26 valid species:

S. ovalis Lewis, 1900 syn. nov. of *S. viaticus* Lewis, 1892.

S. mauritanicus Lewis, 1888 syn. nov. of *S. fuscus* (Schmidt, 1888).

S. aureopilosus Escalera, 1921 syn. nov. of *S. fuscus* (Schmidt, 1888).

S. variolosus Théry, 1921 syn. nov. of *S. alluaudi* Théry, 1921.

S. loustali Kocher, 1956 syn. nov. of *S. alluaudi* Théry, 1921.

S. politus (Schmidt, 1888) syn. nov. of *S. bedeli* (Lewis, 1884).

S. cancer Lewis, 1888 syn. nov. of *S. bedeli* (Lewis, 1884).
S. extructisternum Lewis, 1888 syn. nov. of *S. bedeli* (Lewis, 1884).
S. pectoralis Lewis, 1888 syn. nov. of *S. bedeli* (Lewis, 1884).
S. sedilloti Lewis, 1889 syn. nov. of *S. bedeli* (Lewis, 1884).
S. bonnairei (Schmidt, 1888) syn. nov. of *S. setulosus* (Reitter, 1872).
S. walkeri Lewis, 1888 syn. nov. of *S. setulosus* (Reitter, 1872).
S. fulvus Lewis, 1888 syn. nov. of *S. setulosus* (Reitter, 1872).
S. cancriformis Escalera, 1921 syn. nov. of *S. slaoui* Théry, 1921.

The lectotypes and paralectotypes of the 20 following taxa are designated: *Sternocoelis otini* Peyerimhoff, 1949, *S. marginalis* Normand, 1915, *S. laevidorsis* var. *major* Pic, 1905, *S. laevidorsis* var. *semiopacus* Normand, 1915, *S. viaticus* Lewis, 1892, *S. vaucheri* Lewis, 1896, *S. aureopilosus* Escalera, 1921, *S. alluaudi* Théry, 1921, *S. cancer* Lewis, 1888, *S. walkeri* Lewis, 1888, *S. fulvus* Lewis, 1888, *S. cancriformis* Escalera, 1921, *Hetaerius lewisi* Reitter, 1883, *H. pluristriatus* Fairmaire, 1877, *H. cavisternus* Marseul, 1862, *H. bedeli* Lewis, 1884, *H. politus* Schmidt, 1888, *H. bonnairei* Schmidt, 1888, *H. hispanus* Rosenhauer, 1856 and *Haeterius marseulii* Brisout de Barneville, 1866.

PIC (1937) described *Sternocoelis sulcaticollis* from "environs Maroc: forêt Qaer" (properly: Forêt des Zaër, south of Rabat). This species is characterized by having clearly separated and explanate the sides of pronotum. The remaining characters in the author's description are general for other *Sternocoelis* as well. The description is too imprecise to place it into the key to species without studying it. The present abode of the type is unknown. According to the morphology of sides of pronotum, it could be placed near to *S. otini*, also occurring in Morocco, and may be a synonym. *S. sulcaticollis* has not been considered in this work.

MOTSCHULSKY (1839) briefly described "un nouveau *Haeterius* qui ressemble au *quadratus* Payk., mais mon exemplaire qui vient de Sicile est velu". However the specific name is not quoted; it was included in another work issued in 1858. Therefore the last date should be considered the correct date of publication of *Sternocoelis puberulus*.

ESCALERA (1921) and THÉRY (1921) respectively described *S. cancriformis* and *S. slaoui*, both being synonyms. The work of Théry was included in volume from 1920-1921 dated 1.1.1921 and the work of Escalera was included in volume from 1921 dated 25.4.1921. Thus *S. slaoui* should be considered to have priority on *S. cancriformis*.

PHYLOGENETIC ANALYSIS AND ZOOGEOGRAPHY

Up to now there are scarce data on the phylogeny of Histeridae. HELAVA *et al.* (1985) published an extensive study on the American Hetaeriinae. In this work they argue the hypothesis that the sister-group of the Hetaeriinae are the Exosternini.

According to HELAVA *et al.* (1985) genus *Hetaerius* Erichson, 1834 (Holarctic) and *Mroczkowskiella* Mazur, 1984 (Nearctic) together form the subgroup C3, which is

TABLE 1

Characters employed (Plesiomorphic = 0; Apomorphic = 1, 2, 3)

1. Setae of body: only with long and fine (0); long and short (1); only with short and large (2).
2. Lower part of body: smooth or finely punctate (0); with punctures well impressed and dense (1).
3. Lower part of body: without setae (0); with dense setae (1).
4. Frontal stria: not cariniform on the epistoma (0); being also cariniform on the epistoma (1).
5. Shape of pronotum: trapezoidal, with posterior angles not produced (0); subtrapezoidal, with posterior angles produced (1); sides parallel, with posterior angles produced (2).
6. Sides of pronotum: explanate, clearly separated from disc (0); medially not separated from disc (1).
7. Sides of pronotum: with marginal stria variably reduced (0); without marginal stria (1).
8. Anterior angles of pronotum: not elevated (0); elevated (1).
9. Dorsal striae: the first three complete (0); only with the 4th (1); the second and the third reduced (2); without striae (3).
10. First dorsal stria: complete (0); reduced or lacking (1).
11. Elytral striae: indicated by rows of long setae (0); not indicated by rows of long setae (1).
12. Marginal elytral and outer subhumeral striae: cariniform (0); lacking (1).
13. Epipleural elytral striae: distinct, well impressed (0); reduced (1); lacking (2).
14. Inner prosternal striae: joined or almost joined in front (0); sinuate (1); parallel or apically divergent (2).
15. Inner prosternal striae: fine but complete (0); obsolete, indistinct (1); cariniform (2); with lateral projections (3).
16. Prosternal lobe: slightly sinuate or with medial depression (0); deeply emarginate (2); neither sinuate nor emarginate (1).
17. Prosternal lobe and keel: at same or similar level (0); at very different level (lobe either at lower or at upper level) (1).
18. Prosternal lobe and keel: without depression between them (0); with a shallow depression (1); with deep depression (2).
19. Prosternal base: equally situated than the rest of keel (0); depressed, sloped in relation to keel, directed toward mesosternum (1).
20. Prosternal keel: flat or somewhat convex (0); strongly convex (1).
21. Outer prosternal striae: variably distinct (0); indistinct or very reduced (1).
22. Meso-metasternal excavation: shallow (0); deep, situated on the meso-metasternal suture (1); very deep, on all the metasternal disc (2).
23. Lateral mesosternal foveae: without (0); oblique (1); inside of body (2).
24. Inner lateral stria of metasternum: complete (0), reduced (1); indistinct (2).
25. Meso- and metatibiae: short and enlarged (0); long and weakly enlarged (1); very long and not enlarged (2).

not defined by a synapomorphy. This author considers these taxa to be monophyletic because they share apomorphic character states with the Palearctic genus *Satrapes* Schmidt, 1885, not studied by Helava.

After studying the Palearctic genera of Hetaeriinae, it is assumed the hypothesis that the sister group of *Sternocoelis* is the genus *Hetaerius* (see figure 69). In the Mediterranean area occur three species of *Hetaerius*: *H. ferrugineus* (Olivier, 1789) (western Palearctic), *H. ottomanus* Mazur, 1981 (Turkey) and *H. plicicollis* Fairmaire, 1876 (Algeria), with a lot of north American species.

TABLE 2

Character state matrix for taxa and characters (Plesiomorphic = 0; Apomorphic = 1, 2, 3).

Taxa	Character number																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. viaticus</i>	0	0	0	0	1	1	1	0	2	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	0
<i>S. marseulii</i>	0	0	0	1	1	1	0	1	2	0	0	0	0	0	0	1	0	0	0	0	1	0	0	2	0
<i>S. vaucheri</i>	0	0	0	0	1	1	0	0	2	0	0	0	0	0	0	1	0	0	0	0	1	0	0	2	0
<i>S. lewisi</i>	2	1	0	0	0	1	0	1	2	0	1	0	2	0	0	1	0	0	0	0	0	1	0	1	0
<i>S. diversepunctatus</i>	2	1	0	0	0	1	0	1	2	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0
<i>S. puberulus</i>	2	0	0	0	0	1	0	0	2	0	1	0	1	2	1	0	1	0	0	0	1	0	0	1	0
<i>S. merklii</i>	2	1	0	1	0	1	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0
<i>S. otini</i>	2	0	0	0	0	0	0	0	2	0	1	0	2	1	1	1	1	1	0	0	0	1	0	0	0
<i>S. marginalis</i>	1	0	0	0	0	0	0	0	2	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0
<i>S. laevidorsis</i>	2	0	0	1	0	0	0	0	2	1	1	0	1	1	1	1	0	1	1	0	1	1	0	0	0
<i>S. grandis</i>	2	1	0	1	0	0	0	0	2	1	1	0	0	2	1	0	1	0	0	1	1	1	0	0	0
<i>S. robustus</i>	2	1	1	1	0	0	0	0	2	0	1	0	1	1	1	0	0	1	0	1	1	1	0	1	0
<i>S. fuscus</i>	2	1	0	1	1	1	0	0	2	0	1	0	1	1	2	1	1	1	0	0	0	2	0	1	0
<i>S. incisus</i>	2	0	0	1	1	1	0	1	2	0	1	0	1	1	3	1	0	2	0	0	0	2	1	0	0
<i>S. alluaudi</i>	2	1	0	1	1	0	1	2	0	1	0	2	1	3	0	0	2	0	0	0	2	1	1	0	0
<i>S. acutangulus</i>	2	0	0	1	2	1	0	1	2	0	1	0	2	1	3	0	0	2	0	0	0	2	1	1	0
<i>S. pluristriatus</i>	2	0	0	1	0	1	0	1	1	0	1	0	2	1	2	0	0	0	0	0	0	2	1	1	0
<i>S. bedeli</i>	2	0	0	1	1	1	0	1	2	0	1	0	2	1	2	0	0	0	0	0	0	2	1	1	0
<i>S. punctulatus</i>	0	0	0	1	1	1	0	1	2	0	0	0	2	1	2	0	0	0	0	0	0	2	1	1	0
<i>S. atlantis</i>	1	1	1	1	1	0	1	2	0	1	0	2	2	1	0	1	0	0	0	0	0	2	1	2	1
<i>S. setulosus</i>	1	1	1	1	1	1	0	1	2	0	1	0	2	1	0	0	0	1	0	0	0	2	1	0	1
<i>S. hispanus</i>	1	1	1	0	2	1	0	1	2	0	1	0	2	1	0	0	1	1	0	0	0	2	1	2	1
<i>S. arachnoides</i>	0	0	1	1	2	1	0	1	2	0	1	0	1	2	0	0	1	1	1	1	0	2	2	1	2
<i>S. slaoui</i>	1	0	1	0	1	1	0	1	2	0	1	0	2	2	0	0	1	1	1	1	0	2	2	0	2
<i>S. comosellus</i>	1	0	1	0	2	1	1	0	3	1	1	1	2	2	0	2	1	1	0	0	0	0	0	1	2
<i>S. espadaleri</i>	1	0	1	1	2	1	1	1	2	1	1	0	2	2	0	2	1	0	1	0	0	2	1	1	2

Sternocoelis formerly consists of an array of species defined on the basis of differences in punctuation and setal density. Both characters were found to be highly variable.

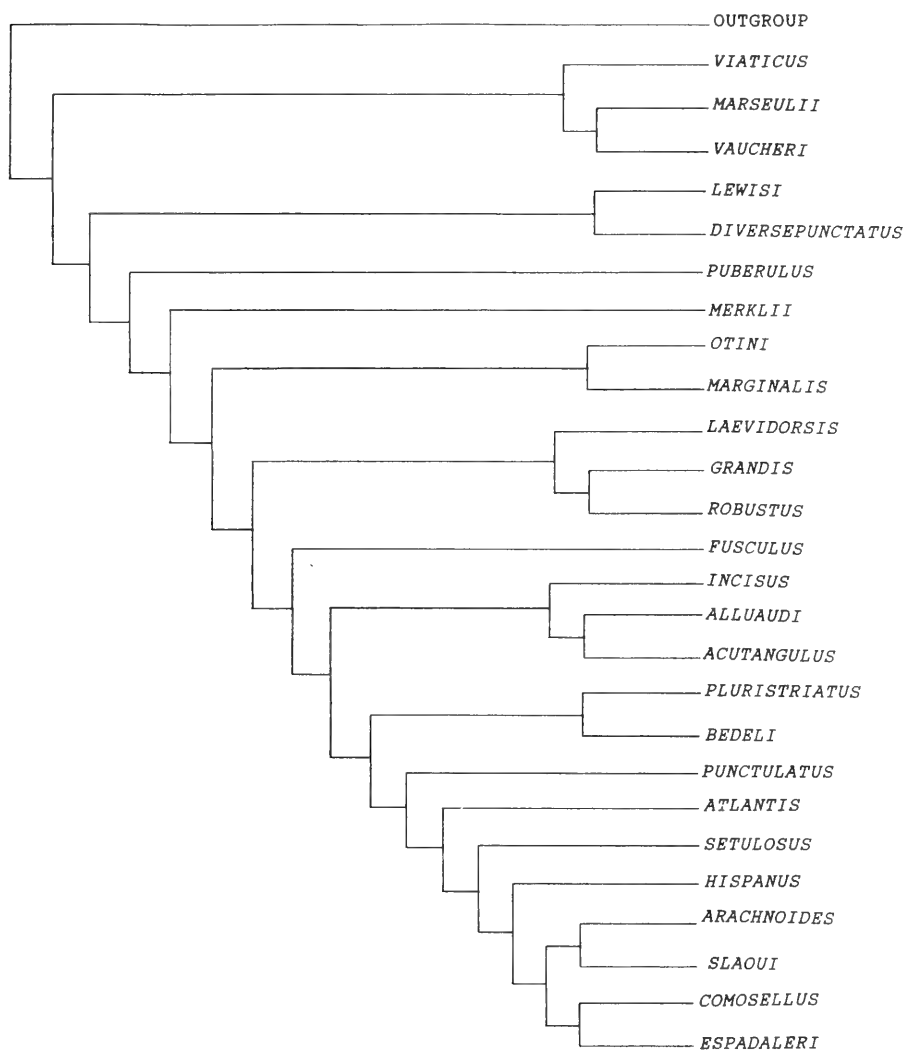
There are several characters which are constant at the species level: general morphology of body, sides of pronotum, elytral striae, prosternum, mesosternum, metasternum and legs. Moreover male genitalia are very constant, with an almost imperceptible intraspecific variability.

Cladistic analysis of the 26 species of *Sternocoelis* was performed using HENNIG'86 (FARRIS, 1988). Twenty-five multistate characters were used for 26 taxa. The relatively low number of characters is due in part to the morphological uniformity of the genitalia.

The taxa were examined to determine the states of the characters from table 1 to construct the matrix (table 2). The hypothesis on character state polarity are listed in table 1 and are based upon a comparison with the chosen outgroup, the west Palaearctic *Hetaerius*.

TABLE 3

The most parsimonious cladogram by the Hennig'86 program from the character matrix included in table 2.



The characters are treated as additive, characters 22 and 23 are weighted three times and 5 and 6 are weighted twice the other characters. Character 22 (meso-metasternal excavation) separate *Hetaerius* and *Sternocoelis*, with a distinct progression among *Sternocoelis* species. Character 23 (lateral mesosternal foveae) show three well-defined morphological types. Character 5 (shape of pronotum) and 6 (sides of

TABLE 4

Geographical distribution of *Sternocoelis* (P = Portugal; GB = Gibraltar; SP = Spain; M = Morocco; A = Algeria; TN = Tunisia; CO = Corsica; SA = Sardinia; SI = Sicily; GR = Greece; B = Bulgaria; TU = Turkey; CY = Cyprus; J = Jordan).

	P	GB	SP	M	A	TN	CO	SA	SI	GR	B	TU	CY	J
<i>S. viaticus</i>					X									
<i>S. marseulii</i>			X											
<i>S. vaucheri</i>				X										
<i>S. lewisi</i>										X				
<i>S. diversepunctatus</i>													X	
<i>S. puberulus</i>							X	X	X					
<i>S. merkliei</i>										X	X	X		
<i>S. otini</i>				X										
<i>S. marginalis</i>						X								
<i>S. laevidorsis</i>					X	X								
<i>S. grandis</i>												X		X
<i>S. robustus</i>													X	
<i>S. fuscus</i>		X	X	X										
<i>S. incisus</i>			X											
<i>S. alluaudi</i>				X										
<i>S. acutangulus</i>		X	X	X										
<i>S. pluristriatus</i>					X									
<i>S. bedeli</i>					X									
<i>S. punctulatus</i>					X									
<i>S. atlantis</i>				X										
<i>S. setulosus</i>					X	X								
<i>S. hispanus</i>	X		X	X										
<i>S. arachnoides</i>			X	X										
<i>S. slaoui</i>				X										
<i>S. comosellus</i>					X									
<i>S. espadalieri</i>				X										

pronotum) also delimit several groups of species. These characters are more appraised because they delimit groups of species variably related with the outgroup. These characters are considered to be of superior phyletic weight by outgroup comparison (NEFF, 1986). It is assumed the hypothesis that those characters have more evolutionary significance by both general generic and outgroup appraisal.

The m*; bb*; option was used to produce 8 equally most-parsimonious trees of length 147 consistency index of 0.34 and retention index of 0.69. These trees mainly differed in the internal position of several species groups with similar branches. The Nelsen command was then used to obtain a consensus tree (strict) (FARRIS, 1988).

The tree presented (table 3) should be considered only as an approximation of the phylogeny of *Sternocoelis*, due to the low consistency resulting from the limited number of characters evaluated. Other analyses can be also carried out.

Plesiomorphic and apomorphic characters were widely distributed with few apomorphies defining species groups (table 3). One clearly monophyletic group as defined by the length of meso- and metatibiae includes *S. atlantis*, *S. setulosus*, *S.*

hispanus, *S. arachnoides*, *S. slaoui*, *S. comosellus*, *S. espadaleri*). Within this group, *arachnoides* and *slaoui* are sister species by virtue of lacking the inner lateral stria of metasternum. *S. comosellus* and *S. espadaleri* are also sister species by virtue of having widely and deeply emarginate prosternal lobe.

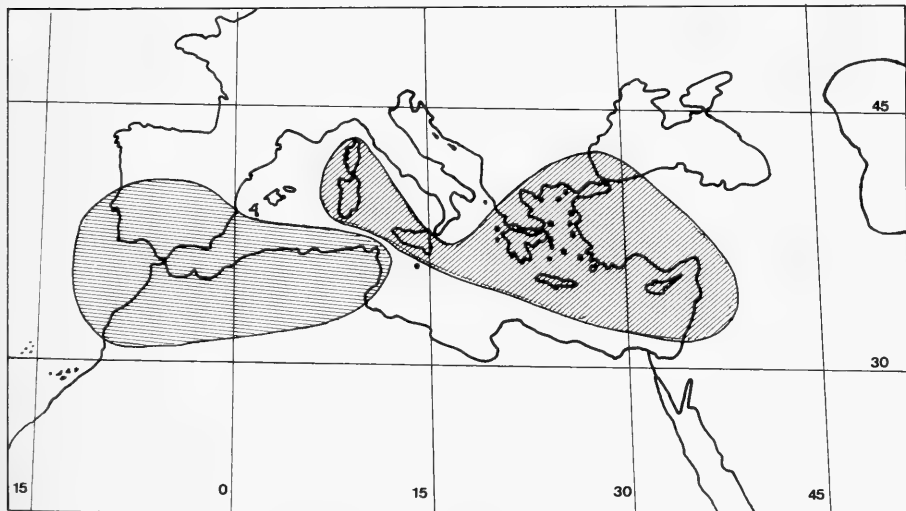
Several plesiomorphic characters occur in all *Sternocoelis*. A plesiotypic clade includes *S. viaticus*, *S. marseulii* and *S. vaucheri*, closely related to the outgroup.

Superposing the cladogram on the geographical distribution of species, two well defined centers of diversity (map 1) can be observed: The first is the Iberian-Maghrebian area including Portugal, Gibraltar, Spain, Morocco, Algeria and Tunisia in which are included the majority of species. The other area in the eastern Mediterranean with fewer species includes Corsica, Sardinia, Sicily, Greece, Bulgaria, Turkey, Cyprus and Jordan. A zone of contact exists for both groups via the Central Mediterranean region (Tunisia, Sicily and Greece). In general, the Iberian-Maghrebian species exhibit a greater frequency of apomorphic characters than the species from the other area. However the most plesiomorphic clade is found here as well.

It seems logical to postulate the origin of this genus in the region of Northern Africa in the vicinity of the Atlas mountains, dispersed from W to E. A dispersion from E to W could also be possible, with the origin in the eastern Mediterranean, but it does not agree with the closeness among the three Iberian-Maghrebian species (*viaticus*, *marseulii*, *vaucheri*) and the outgroup. Early this genus would have been

MAP 1

Distribution of *Sternocoelis* in the Mediterranean area showing two areas (Iberian-Maghrebian and north-eastern).



distributed on the Mediterranean area. The geographical isolation would have confined several species on the central-oriental area, with low specific diversity, showing plesiomorphic characters. Later other species with apomorphies would have been generated, being dispersed on the Iberian-Maghrebian area, not reaching the central-oriental zone due to the new geographical framework. This area is inhabited by both plesiomorphic and apomorphic species and the highest species diversity (table 4). The species with the larger number of apomorphies do not occur in the north-oriental area.

Several instances of possible speciation by vicariance can be observed (CROIZAT *et al.*, 1974). Several groups which may have speciated allopatrically include: [*viaticus* (Algeria)- *marseullii* (Spain)- *vaucheri* (Morocco)], [*puberulus* (Sicily, Sardinia, Corsica)- *merklII* (Greece, Bulgaria, Turkey)], [*otini* (Morocco)- *marginalis* (Tunisia)], [*grandis* (Turkey, Jordan)- *robustus* (Cyprus)], [*diversepunctatus* (Cyprus)- *lewisi* (Greece)], [*atlantis* (Morocco)- *setulosus* (Algeria, Tunisia)- *hispanus* (Portugal, Spain, Morocco)] and [*comosellus* (Algeria)- *espadaleri* (Morocco)]. Groups which may have speciated sympatrically include: [*pluristriatus*- *bedeli* (Algeria)], [*arachnoides* (South Spain, North Morocco)- *slaoui* (North Morocco)].

According to the cladogram *Sternocoelis* is divided into two major monophyletic lineages. The plesiotypic *viaticus*-group and a much larger group composed of the remainder species. The larger group is subdivided into the following species groups: *S. merklII*-group, six species; *S. otini*-group, three species; and the *S. fuscus*-group fourteen species.

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Agathidiini from Taiwan collected by Dr. Ales Smetana (Coleoptera, Leiodidae, Agathidiini)

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Agathidiini from Taiwan collected by Dr. Ales Smetana (Coleoptera, Leiodidae, Agathidiini). - Descriptions and/or field data are presented for 49 species of *Agathidiini* from Taiwan based on 392 specimens collected in 1990 and 1991 by Dr. Ales Smetana.

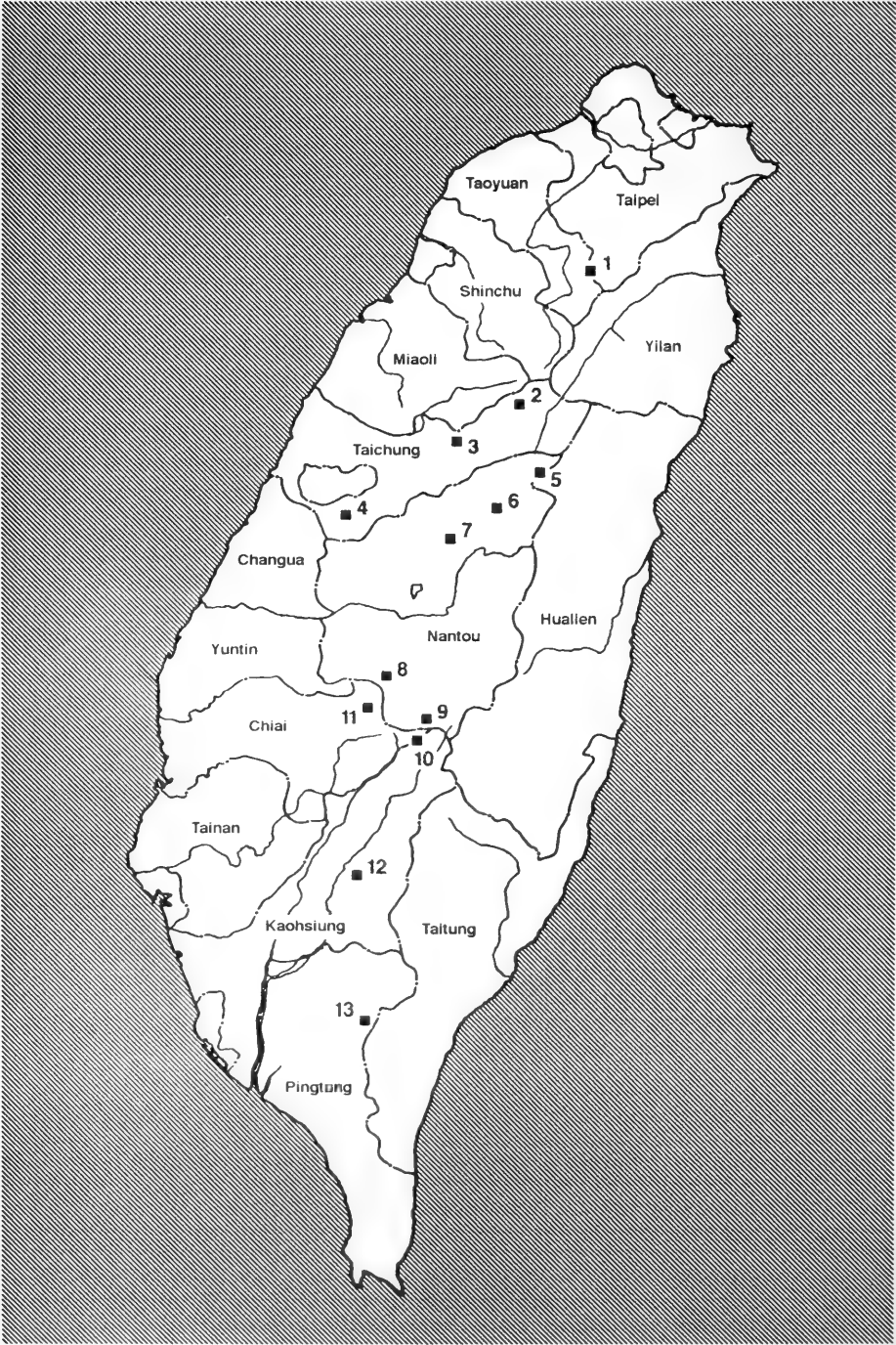
New species: *Anisotoma smetanai* n.sp., *Cyrtoplastus smetanai* n.sp., *Agathidium yushanicum* n.sp., *A. inquisitor* n.sp., *A. geniculatum* n.sp., *A. praestum* n.sp., *A. nigrocastaneum* n.sp., *A. tarokoense* n.sp., *A. vestitum* n.sp., *A. rufomarginatum* n.sp., *A. oblitum* n.sp., *A. tardum* n.sp., *A. distinguendum* n.sp., *A. familiare* n.sp., *A. glabricolle* n.sp., *A. honestum* n.sp., *A. lucidum* n.sp., *A. tenebroides* n.sp., *A. discretum* n.sp., *A. meifengense* n.sp., *A. tessellatum* n.sp., *A. memnonium* n.sp., *A. kaohsiungense* n.sp., *A. chalconotum* n.sp., *A. angustatum* n.sp., *A. fuliginosum* n.sp., *A. alpestre* n.sp., *A. furcatum* n.sp., *A. comptum* n.sp., *A. egregium* n.sp., *A. anmahhanense* n.sp., *A. subalpinum* n.sp., *A. intricatum* n.sp., *A. inustum* n.sp., *A. taichungense* n.sp., *A. exoletum* n.sp., *A. fuscum* n.sp., *A. lunatum* n.sp., *A. umbratum* n.sp., *A. fenestratum* n.sp., *A. asphaltinum* n.sp., *A. splendidulum* n.sp., *A. melanocephalum* n.sp., *A. chiaicum* n.sp., *A. amictum* n.sp., *A. venustum* n.sp.

New generic record from the Oriental region: *Cyrtoplastus*.

Key-words: Leiodidae - *Agathidiini* - Taiwan - new species.

INTRODUCTION

The present paper describes the material of *Agathidiini* collected by Dr. Ales Smetana in 1990 (14.IV-12.V) and 1991 (7.V-23.V) in 40 different localities of Taiwan. Fortynine species are treated, 46 of which are new to science. Among these, the following species are particularly remarkable for the Oriental region:



- one new species of *Anisotoma*, as only another species of this genus was known;

- one new species of *Cyrtoplastus*, as no species of this genus was known;

- three new species of *Agathidium* subg. *Cyphocele*, as only another species of this subgenus was known.

Other reports include 5 species of *Agathidium* subg. *Neoceble*, rare in the Oriental region, and 3 out of 6 species already known for Taiwan.

The specimens are deposited in the Natural History Museum of Geneva (MHNG), National Museum of Natural Science in Taichung (NMNT) and Angelini's collection (AC).

We wish to express our sincerest thanks to Dr. Ales Smetana (Ottawa) for both the loan of this precious material and his generous assistance in editing the paper.

KEY TO THE AGATHIDIINI OF TAIWAN

- | | | |
|----|---|--------------------------------|
| 1 | Antennal club 5-segmented. Genus <i>Anisotoma</i> | <i>smetanai</i> n.sp. |
| 1' | Antennal club 4- or 3-segmented. | 2 |
| 2 | Antennal club 4-segmented. Genus <i>Afroagathidium</i> . . . | <i>orientale</i> Ang. & Dmz. |
| 2' | Antennal club 3-segmented. | 3 |
| 3 | Postocular carina absent. Genus <i>Liodopria</i> | <i>taiwanensis</i> Ang. & Dmz. |
| 3' | Postocular carina present. | 4 |
| 4 | Clypeus protuberant (fig. 9). Genus <i>Cyrtoplastus</i> | <i>smetanai</i> n.sp. |
| 4' | Clypeus not protuberant. Genus <i>Agathidium</i> | 5 |
| 5 | Elytra with sharp humeral angle. Metasternum without femoral lines. | 6 |
| 6 | Head with temples 1/2 length of eye (fig. 14). Subg. <i>Cyphocele</i> | 7 |
| 7 | Body length: 4,5-5,1 mm. | <i>yushanicum</i> n.sp. |
| 7' | Body length: 2,5-3,4 mm. | 8 |

MAP 1

Localities in Taiwan - 1, Taoyuan Hsien, Takuanshan Forest, 1650 m, 17.IV.1990; 2, Taichung Hsien, Hsuehshan, near Hsuehshan Tun-Feng, 3170 m, 7.V.1991; above Shan-Liu Gieu Hut, 3220 m, 7-8.V.1991; near Hsuehshan Tun-Feng, 3170 m, 11.V.1991; 3, Anmashan, 2225 m, 1-4.V.1990; 4, Wufeng, 100-200 m, 14-15.IV.1990; 5, Nantou Hsien, Houhuanshan, 3100 m, 20.IV.1990; 6, Meifeng, 2130 m, 3, 12-13.V.1991; 7, Fengnan, 700 m, 22.IV.1990; 8, San-liu-chiu (Shanlinchi), 1650 m, 16.IV.1990; 9, Yushan, SW slope below Yushan Mn. peak, 3650-3720 m, 14-15.V.1991; Pai-Yun Hut, 3528 m, 15.V.1991; 2 Km W Pai-Yun Hut, 3350 m, 16.V.1991; 1,8 Km W Pai-Yun Hut, 3375 m, 17.V.1991; 10, Chiai Hsien, Yushan N. P., Ta-Ta Ghia, 2750 m, 27.IV.1990; Mun-Li Cliff, 1700-2700 m, 27.IV.1990, 13.V.1991 and 18.V.1991; Taroko N.P., Nanhushi Hut, 2220 m, 8.V.1990; Chungyantienshi river, 2280 m, 10.V.1990; ridge SE Nanhushi Hut, 2700 m, 11.V.1990; Nanhushi Hut, 2220 m, 12.V.1990; 11, Alishan, Sister Ponds, 2180 m, 26.IV.1990; 12, Kaohsiung Hsien, Tienchih (Tengchih), 1535-1800 m, 23-24.IV.1990; 13, Pingtung Hsien, Peitawushan, Kuai-Ku Hut, 2325 m, 21.V.1991; above Kuai-Ku Hut, 2325 m, 22.V.1991; trail at 2000 m, 23.V.1991.

- 8 Body length: 3,4 mm; 3rd antennal segment 2,4 times as long as 2nd; head and pronotum black, elytra reddish-brown; two sizes of punctures on head and pronotum. *inquisitor* n.sp.
- 8' Body length: 2,5-2,8 mm. *geniculatum* n.sp.
- 6' Head without temples, widest either at eyes or at posterior margin of eyes (figs 31-34). Subg. *Neoceble*. 9
- 9 Body length: 3,3 mm. *praeustum* n.sp.
- 9' Body length: 2,1-2,8 mm. 10
- 10 Third antennal segment 1,5 times as long as 2nd. *nigrocastaneum* n.sp.
- 10' Third antennal segment 0,7-1,0 times as long as 2nd. 11
- 11 Entire dorsum black and microreticulate; 3rd antennal segment 0,7 times as long as 2nd. *tarokoense* n.sp.
- 11' Dorsum with microreticulation absent or vague; dorsum reddish-brown; 3rd antennal segment as long as 2nd. 12
- 12 Antennae uniformly testaceous; female tarsal formula: 5-4-4; head widest at eyes (fig. 33). *vestitum* n.sp.
- 12' Antennae darker at club; female tarsal formula: 4-4-4; head widest at posterior margin of eyes (fig. 34). *rufomarginatum* n.sp.
- 5' Elytra with weak humeral angle. Metasternum either with femoral lines or greatly abbreviated and without distinct femoral lines. 13
- 13 Metasternum greatly abbreviated: femoral lines indistinct. Subg. *Macroceble*. *oblitum* n.sp.
- 13' Metasternum not greatly abbreviated: femoral lines distinct. 14
- 14 Eyes flattened or moderately protuberant; clypeal line either typical (= semicircular, more or less impressed line) or absent; pronotum 1,3-1,7 times as wide as head. Subg. *Agathidium* s.str. 15
- 15 Antero-lateral margins of head raised. Group: *madurensis*. 16
- 16 Third antennal segment 1,8 times as long as 2nd. *tardum* n.sp.
- 16' Third antennal segment 1,1-1,3 times as long as 2nd. 17
- 17 Entire dorsum black; antennae uniformly testaceous; male hind femora with a sharp tooth. *distinguendum* n.sp.
- 17' Entire dorsum reddish-brown; antennae darker at segments 7-10; male hind femora without tooth. 18
- 18 Third antennal segment 1,3 times as long as 2nd; pronotum not markedly broader than long ($W/L = 1,35$); metathoracic wings present; lateral lines of mesosternum incomplete. *formosum* Ang. & Dmz.
- 18' Third antennal segment as long as 2nd; pronotum moderately broader than long ($W/L = 1,51$); metathoracic wings absent; lateral lines of mesosternum absent. *familiale* n.sp.
- 15' Antero-lateral margins of head not raised. 19
- 19 Sutural striae present. Dorsum microreticulate. Group: *seminulum*. *glabricolle* n.sp.
- 19' Sutural striae absent. 20
- 20 Dorsum microreticulate. Group: *laevigatum*. 21

- 21 Third antennal segment 0,9-1,0 times as long as 2nd. 22
- 22 Dorsum reddish-brown, male hind femora with very sharp tooth (fig. 95); mesosternum with a raised median carina. *honestum* n.sp.
- 22' Dorsum black; male hind femora without tooth; mesosternum without median carina. 23
- 23 Eyes protuberant (fig. 66); proximal part of aedeagus simple (fig. 78). *lucidum* n.sp.
- 23' Eyes flattened (fig. 67); proximal part of aedeagus hook-like (fig. 104). *tenebroides* n.sp.
- 21' Third antennal segment 1,1-1,8 times as long as 2nd. 24
- 24 Third antennal segment 1,8 times as long as 2nd. Male copulatory organ: figs 107-109. *discretum* n.sp.
- 24' Third antennal segment 1,1-1,7 times as long as 2nd. 25
- 25 Body length: 4,1 mm. *meifengense* n.sp.
- 25' Body length: 2,5-3,6 mm. 26
- 26 Male hind femora simple. 27
- 27 Body length: 2,9-3,2 mm; 3rd antennal segment 1,4 times as long as 2nd; pronotum moderately broader than long (W/L = 1,36); eyes flattened (fig. 68). *tessellatum* n.sp.
- 27' Body length: 3,3-3,5 mm; 3rd antennal segment 1,3 times as long as 2nd; pronotum not markedly broader than long (W/L = 1,27); eyes protuberant (fig. 70). *memnonium* n.sp.
- 26' Male hind femora either with a sharp tooth or enlarged distally. 28
- 28 Male hind femora enlarged distally, without a true tooth. 29
- 29 Body length: 3,0-3,1 mm. Entire dorsum black; eyes protuberant (fig. 121); 3rd antennal segment 1,2 times as long as 2nd. *kaohsiungense* n.sp.
- 29' Body length: 2,8 mm. Entire dorsum reddish-brown; eyes protuberant (fig. 122); 3rd antennal segment 1,5 times as long as 2nd. *chalconotum* n.sp.
- 28' Male hind femora with a more or less sharp tooth. 30
- 30 Male hind femora with a small subdistal tooth (figs 127-132). 31
- 31 Male hind femora with a hook-like tooth (figs 127-128). 32
- 32 Eyes moderately protuberant (fig. 123); median carina of mesosternum raised; entire dorsum dark reddish-brown; body length: 2,9-3,4 mm. *angustatum* n.sp.
- 32' Eyes more protuberant (fig. 124); median carina of mesosternum weak; entire dorsum black; body length 3,5 mm. *fuliginosum* n.sp.
- 31' Male hind femora with an usual tooth (fig. 129-132). 33
- 33 Body length 3,0-3,2 mm; entire dorsum black. *alpestre* n.sp.
- 33' Body length 2,5-2,8 mm; entire dorsum reddish-brown. 34
- 34 Parameres with a preapical enlargement (fig. 160). *furcatum* n.sp.
- 34' Parameres evenly narrowing toward apex. 35
- 35 Male copulatory organ as in figs 163-165. *comptum* n.sp.
- 35' Male copulatory organ as in figs 166-168. *egregium* n.sp.

- 30' Male hind femora with a very large tooth (figs 133-138). 36
- 36 Median carina of mesosternum absent. *anmashanense* n.sp.
- 36' Median carina of mesosternum present. 37
- 37 Pronotum moderately broader than long ($W/L = 1,18-1,21$), markedly bent at anterior margin (figs 175-176). 38
- 38 Eyes moderately convex (fig. 125); male copulatory organ: figs 172-174; male tarsi much more enlarged than those of females. . . *subalpinum* n.sp.
- 38' Eyes more convex (fig. 126); male copulatory organ: figs 201-203; male tarsi moderately more enlarged than those of females. . . *intricatum* n.sp.
- 37' Pronotum sharply broader than long ($W/L = 1,27-1,46$), moderately bent at anterior margin (figs 177-178). 39
- 39 Body length 2,7-3,0 mm; 3rd antennal segment 1,6 times as long as 2nd. *inustum* n.sp.
- 39' Body length 3,3-3,6 mm; 3rd antennal segment 1,1-1,3 times as long as 2nd. . 40
- 40 Pronotum moderately broader than long ($W/L = 1,29$); its lateral outline as in fig. 177; elytra broader than long ($W/L = 0,87$). *taichungense* n.sp.
- 40' Pronotum sharply broader than long ($W/L = 1,46$); its lateral outline as in fig. 178; elytra as broad as long. *exoletum* n.sp.
- 20' Dorsum not microreticulate. Group: *dentatum*. 41
- 41 Body length 4,0-4,2 mm. 42
- 42 Male hind femora with a small subdistal tooth (figs 193-194); 3rd antennal segment 1,6-1,8 times as long as 2nd. 43
- 43 Third antennal segment 1,8 times as long as 2nd; pronotum vaguely broader than long ($W/L = 1,06$). *fuscum* n.sp.
- 43' Third antennal segment 1,6 times as long as 2nd; pronotum slightly broader than long ($W/L = 1,16$). *lunatum* n.sp.
- 42' Male hind femora with a sharp tooth (figs 195-200); 3rd antennal segment 1,4-1,5 times as long as 2nd. 44
- 44 Apex of aedeagus slightly bent up (fig. 223); elytra markedly broader than long ($W/L = 1,21$); eyes moderately protuberant (fig. 187). *umbratum* n.sp.
- 44' Apex of aedeagus sharply bent up (fig. 226); elytra as broad as long; eyes flattened (fig. 189). *fenestratum* n.sp.
- 41' Body length 3,0-3,9 mm. 45
- 45 Third antennal segment as long as 2nd. *asphaltinum* n.sp.
- 45' Third antennal segment 1,25-1,54 times as long as 2nd. 46
- 46 Male hind femora with very sharp tooth (fig. 198); 3rd antennal segment 1,54 times as long as 2nd; parameres with a sharp subapical enlargement (fig. 232). *splendidulum* n.sp.
- 46' Male hind femora with a comparatively small subdistal tooth (figs 199-200); 3rd antennal segment 1,27 times as long as 2nd; parameres without subapical enlargement. 47
- 47 Male copulatory organ as in figs 235-237; spermatheca as in fig. 244. *melanocephalum* n.sp.

- 47' Male copulatory organ as in figs 238-240; spermatheca as in fig. 245.
..... *chiaicum* n.sp.
- 14' Eyes hemispherical (figs 247, 251); clypeal line atypical (= either a continuous or interrupted crest, or a couple of short grooves); pronotum 1,7-2,1 times as broad as head. Subg. *Microceble*. 48
- 48 Head at least partly striolate. 49
- 49 Head striolate only at clypeus; pronotum without microreticulation.
..... *klapperichi* Ang. & Dmz.
- 49' Head striolate on entire surface; pronotum with superficial microreticulation. 50
- 50 Male copulatory organ: see Cooter, 1984. *puncticollis* Cooter
- 50' Male copulatory organ as in figs 254-256. *amicum* n.sp.
- 48' Head not striolate. 51
- 51 Male copulatory organ: see Angelini & De Marzo, 1985.
..... *taiwanense* Ang. & Dmz.
- 51' Male copulatory organ as in figs 258-260. *venustum* n.sp.

Genus *Anisotoma* Panzer, 1797

Anisotoma smetanai n.sp.

Figs. 1-6

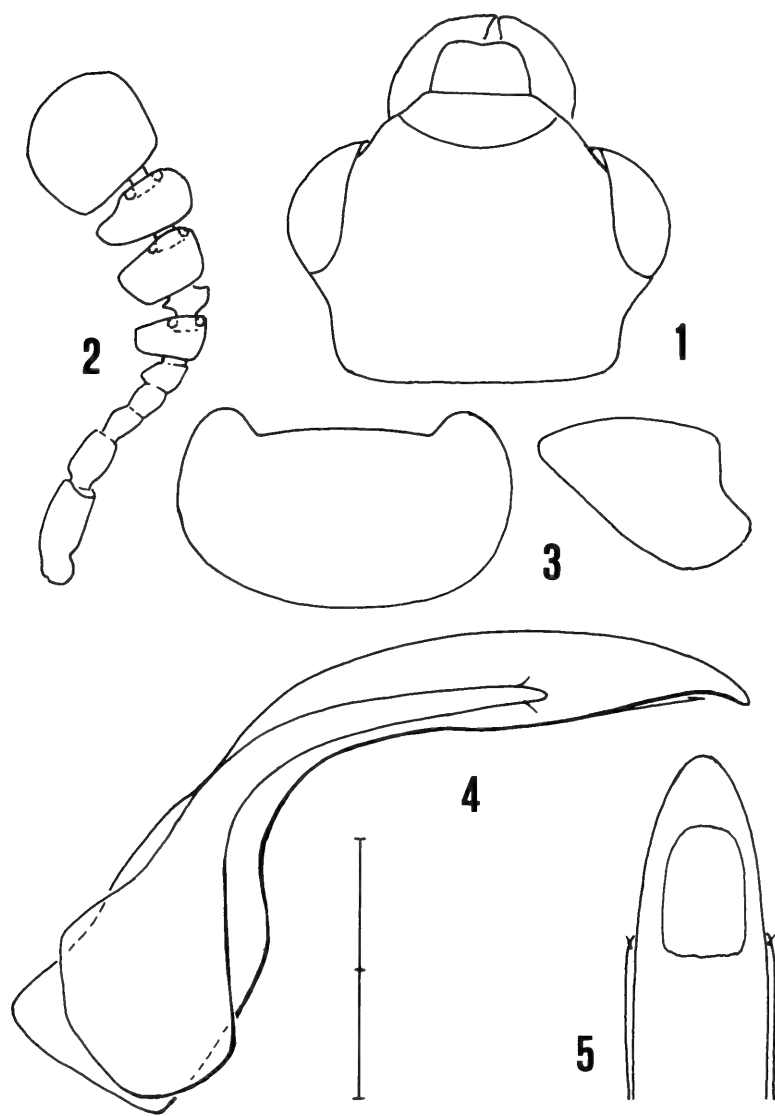
Length 2,2-2,4 mm (holotype ♂ 2,25 mm). Dorsum of head black, reddish-brown near anterior margin; pronotum and elytra reddish-brown; venter reddish-brown, paler at mesosternum; antennae darker at segments 8-10; legs reddish-brown. Microreticulation absent on entire dorsum; puncturation well impressed on head and elytra, weaker on pronotum; two sizes of punctures on elytra. Antennae 10-segmented in both sexes; Hamann's organ: gutter without vesicles in 6th, 8th and 9th segments.

Head: Widest at eyes (fig. 1); eyes hemispherical; clypeus moderately protruding, without a pit at each side; clypeal line shallow. Antennae 10-segmented (fig. 2). Microreticulation absent; punctures moderately large and impressed, spaced from each other by 2-3 times their own diameter.

Pronotum: 1,53 times as broad as head, markedly broader than long ($W/L = 1,92$), vaguely convex ($W/H = 2,38$). Dorsal and lateral outlines: fig. 3. Punctures of half size of those on head, impressed, spaced from each other by 2-3 times their own diameter; sparse, very small punctures are interposed. Holotype: length 0,52 mm, width 1,00 mm, height 0,42 mm.

Elytra: Moderately broader than pronotum, as broad as long, slightly convex ($W/H = 1,52$); lateral outline with sharp humeral angle; sutural striae weak, confined to apical half of elytra. Two sizes of punctures; punctures of larger size as large as those on head, spaced from each other by 0,5-2 times their own diameter; punctures of smaller size of nearly half diameter and sparser. Holotype: length 1,20 mm, width 1,22 mm, height 0,80 mm.

Metathoracic wings present. Meso- and metasternum: median carina absent, lateral lines complete, femoral lines absent.



FIGS 1-5

Anisotoma smetanai n.sp.: head, antenna, pronotum (dorsal and lateral outline) and male copulatory organ (lateral view and ventral view of its apex). Scale: 1 division = 0,1 mm.

Legs: Tarsal formula: ♂ 4-4-4, ♀ 4-4-4; male tarsi not larger than those of females.

Male copulatory organ (figs 4-5): Aedeagus slender, with proximal part simple and apex bent down, lateral margins gently converging toward broadly rounded apex, ventral piece weakly sclerotized, not bifid. Parameres slender, short, gently narrowing toward apex.

Spermatheca (fig. 6): Both basal and apical parts stout, the former longer.

HOLOTYPE ♂: Hualien Hsien, Taroko N. P., Nanhushi Hut, 2220 m, 12.V.1990, in MHNG.

PARATYPE: Anmashan, 2225 m, 3.V.1990, 1 ♀, in AC.

Discussion: *Anisotoma smetanai* n.sp. easily differs from the two other species of this genus which occur in SE Asia, *A. martensi* Ang. & Dmz. (1994: 2, Nepal) and *A. loebli* Ang. & Dmz. (1986b: 828, Nepal) by its 10-segmented antennae; it differs from *A. loebli* in the dorsal coloration and from *A. martensi* in the size. The puncturation and the antennal club coloration are similar.

Habitats: Original broad-leaved forest, around bases of large trees. Original coniferous forest, rotting bark, wood and various debris near bases of large trees.

Distribution: Taiwan.

Etymology: dedicated to Dr. Ales Smetana, who found this species.

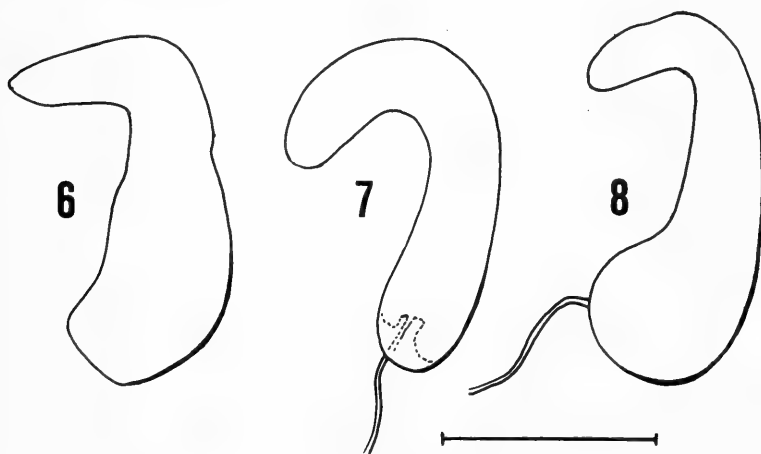
Genus **Liodopria** Reitter, 1909

Liodopria taiwanensis Ang. & Dmz.

Fig. 7

Liodopria taiwanensis Angelini & De Marzo, 1985, Entomologica, 19: 24.

Material: Nantou Hsien, Yushan N. P., SW slope below Yushan Mn. peak., 3650 m, 14.V.1991, 1 ♀ in MHNG.



FIGS 6-8

Spermatheca of: 6, *Anisotoma smetanai* n.sp.; 7, *Liodopria taiwanensis* Ang. & Dmz., 8, *Cyrtoplastus smetanai* n.sp. Scale: 1 division = 0,1 mm.

Discussion: The spermatheca of *Liodopria taiwanensis* Ang. & Dmz. (1985: 25; Taiwan) is figured here again, because its shape is appreciably different in the present specimen.

Habitat: Subalpine zone, moss, mouldy litter, humus and various debris under dense bushes of *Rhododendron*, with intermixed junipers.

Distribution: Taiwan.

Genus *Cyrtoplastus* Reitter, 1884

Cyrtoplastus smetanai n.sp.

Figs. 8-13

Length 2.4-2.7 mm (holotype ♂ 2.50 mm). Dorsum of head dark reddish-brown; pronotum and elytra reddish-brown; venter black, paler at mesosternum; antennae testaceous, darker at segments 9-10; legs reddish-brown. Microreticulation absent on entire dorsum, except for some traces on elytra; two sizes of punctures on head; puncturation fine on pronotum, very sparse on elytra.

Head: Widest at the posterior margin of eyes (fig. 9); eyes hemispherical; clypeus protruding, without a pit at each side; clypeal line sharp. Antennae 10-segmented; 3rd antennal segment as long as 2nd, longer than 4th and 5th combined (fig. 10); Hamann's organ: gutter without vesicles in both 9th and 10th antennal segments. Punctures of the larger size impressed, spaced from each other by 1-2 times their own diameter; punctures of smaller size very sparse.

Pronotum: 1.73 times as broad as head, markedly broader than long ($W/L = 2.2$), little convex ($W/H = 2.25$). Dorsal and lateral outlines: fig. 11. Punctures as large as those on head, superficial, spaced from each other by 2-10 times their own diameter. Holotype: length 0.60 mm, width 1.32 mm, height 0.63 mm.

Elytra: Moderately broader than pronotum, slightly broader than long ($W/L = 1.08$), very convex ($W/H = 1.32$); lateral outline with sharp humeral angle; sutural striae weak, confined to apical fifth of elytra. Punctures very small, superficial, spaced from each other by 2-10 times their own diameter. Holotype: length 1.35 mm, width 1.46 mm, height 1.10 mm.

Metathoracic wings absent. Meso- and metasternum: median carina absent, lateral lines complete, femoral lines absent.

Legs: Tarsal formula: ♂ 5-5-4, ♀ 4-4-4.

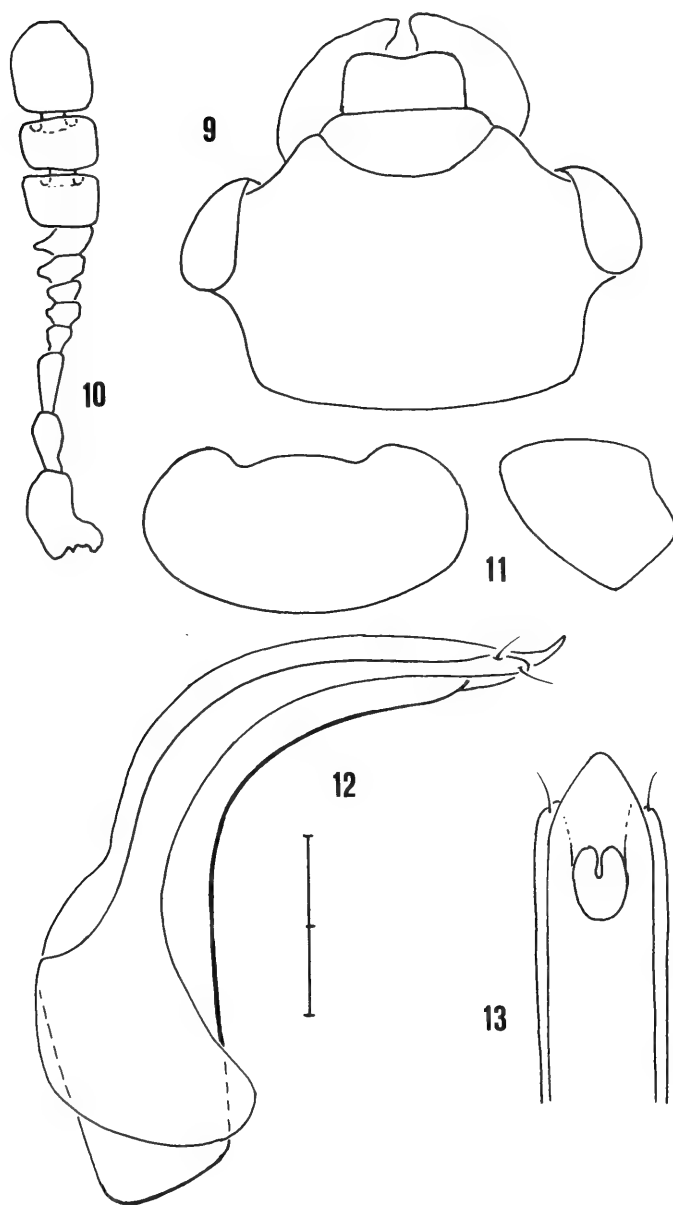
Male copulatory organ (figs 12-13): Aedeagus slender, with proximal part simple and apex bent up, lateral margins parallel and abruptly converging toward subacute apex, ventral piece bifid. Parameres slender, enlarged at apex.

Spermatheca (fig. 8): Both basal and apical parts stout; the former longer.

HOLOTYPE ♂: Taoyuan Hsien, Takuanshan For., 1650 m, 17.IV.1990, in MHNG.

PARATYPES: Together with the holotype, 1 ♂ in MHNG, 1 ♀ in NMNT, 1 ♂ and 1 ♀ in AC; Taichung Hsien, Anmashan, 2225 m, 3.V.1990, 1 ♀ in MHNG.

Discussion: *Cyrtoplastus smetanai* n.sp. may be easily separated from the other Agathidiini of SE Asia by the generic characters (see key to species). If it is compared to *C. seriepunctatus* Bris., the elytral puncturation and size are clearly



FIGS 9-13

Cyrtoplastus smetanai n.sp.: head, antenna, pronotum (dorsal and lateral outline) and male copulatory organ (lateral view and ventral view of its apex). Scale: 1 division = 0,1 mm.

different in both species, although their male copulatory organs and spermathecae are similar. *C. smetanai* differs from *C. laevis* Hisamatsu 1985 (Japan) by the absence of punctured striae on the elytra.

Habitat: Original broad-leaved forest, mouldy layers of fallen leaves and twigs around bases of large trees, debris and humus among the lush vegetation along a trail.

Distribution: Taiwan.

Etymology: dedicated to Dr. Ales Smetana, who found this species.

Genus **Agathidium** Panzer, 1797

Subg. **Cyphocele** Thomson, 1859

Agathidium (Cyphocele) yushanicum n.sp.

Figs 14, 15, 18-20, 24

Length 4.5-5.1 mm (holotype ♂ 5.0 mm). Entire dorsum and venter reddish-brown; antennae reddish-brown, slightly darker at segments 9 and 10; legs reddish-brown. Microreticulation impressed on head and pronotum, absent on elytra; punctuation fine on head and pronotum, impressed on elytra; two sizes of punctures on the latter.

Head: Widest behind eyes: temple 1/2 length of eye (fig. 14); eyes flattened; clypeus slightly excavated, with a pit at each side; clypeal line sharp. Third antennal segment twice as long as 2nd, as long as 4th and 5th combined. With very impressed microreticulation, opaque; punctures large, superficial, spaced from each other by 1-2 times their own diameter.

Pronotum: 1.52 times as broad as head, sharply broader than long ($W/L = 2.05$) and slightly convex ($W/H = 1.97$). Dorsal and lateral outlines: fig. 15. Microreticulation and punctuation as on head. Holotype: length 1.30 mm, width 2.67 mm, height 1.35 mm.

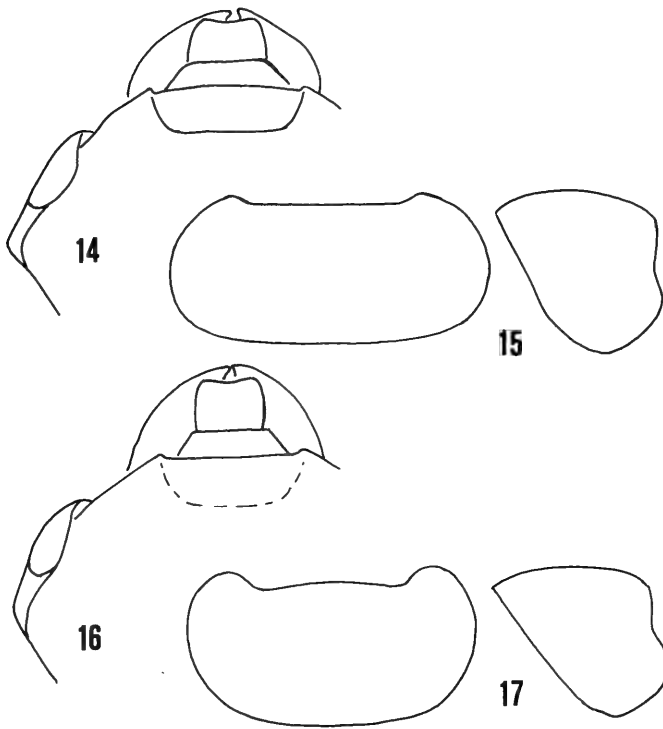
Elytra: Moderately broader than pronotum, slightly broader than long ($W/L = 1.1$) and slightly convex ($W/H = 1.96$); lateral outline with sharp humeral angle; sutural striae weak, confined to apical half of elytra. Punctures very large, impressed, spaced from each other as much as their own diameter. Holotype: length 2.50 mm, width 2.75 mm, height 1.40 mm.

Metathoracic wings: vestigial. Meso- and metasternum: median carina weak, lateral lines complete, femoral lines absent.

Legs: Tarsal formula: ♂ 5-5-4, ♀ 4-4-4; segment 1 of front and middle tarsi dilated in males.

Male copulatory organ (figs 18-20): Aedeagus slender, with proximal part simple and apex bent up, lateral margins parallel and then abruptly converging toward subacute apex, ventral piece indistinct; short endophallic flagellum protruding. Parameres very slender, not enlarged at apex.

Spermatheca (fig. 24): Basal part elongate, twisted at duct connection; apical part stout, shorter.



Figs 14-17

Head and pronotum (dorsal and lateral outline) of: 14-15, *Agathidium yushanicum* n.sp.; 16-17, *A. inquisitor* n.sp.

HOLOTYPE ♂: Nantou Hsien, Yushan N. P., SW slope below Yushan Mn. peak., 3650 m, 14.V.1991, in MHNG.

PARATYPES: Together with the holotype, 10 ♂ and 1 ♀ in MHNG, 1 ♂ and 1 ♀ in NMNT, 3 ♂ and 2 ♀ in AC; same locality, 3720 m, 15.V.1991, 4 ♂ and 1 ♀ in MHNG, 2 ♂ and 2 ♀ in NMNT, 3 ♂ and 1 ♀ in AC; same locality, 3650 m, 15.V.1991, 3 ♂ in MHNG, 1 ♂ and 1 ♀ in NMNT, 2 ♂ and 1 ♀ in AC; same locality, Pai-Yun Hut, 3528 m, 15.V.1991, 2 ♀ in MHNG; same locality 2 Km W Pai-Yun Hut, 3375 m, 17.V.1991, 1 ♂ in MHNG, 1 ♂ in AC; same locality, Mun-Li Cliff, 2700 m, 18.V.1991, 1 ♂ in AC; Taichung Hsien, Annashan, 2225 m, 3.V.1990, 2 ♀ in MHNG; same locality, 2230 m, 4.V.1990, 1 ♂ in MHNG; Hsuehshan, above Shan-Liu Gieu Hut, 3200 m, 8.V.1991, 1 ♂ and 1 ♀ in MHNG; Chiai Hsien, Alishan, Sister Ponds, 2180 m, 26.IV.1990, 1 ♀ in MHNG; Yushan N. P., Ta-Ta Ghia, 2750 m, 27.IV.1990, 1 ♀ in MHNG.

Discussion: *Agathidium yushanicum* n.sp. differs from *A. inquisitor* n.sp. and *A. geniculatum* n.sp. by the size, the microreticulation, by the antennal coloration and by the deeper clypeal line; within the subg. *Cyphoceble*, three Taiwanese species share the dorsal microreticulation, which is lacking in *A. glabrum* Ang. & Dmz. (1986b) from Nepal.

Habitats: Original broad-leaved forest. Subalpine zone, moss, mouldy layers of litter, humus and various debris under dense bushes of *Rhododendron*, with intermixed junipers. Subalpine zone, moss, mouldy litter, humus and various debris under dense junipers with intermixed *Rhododendron* bushes. Original *Abies* forest, rotting bark and wood along fallen trees. Original coniferous forest (mainly *Chamaecyparis*), moss and plant debris.

Distribution: Taiwan.

***Agathidium (Cyphocele) inquisitor* n.sp.**

Figs. 16, 17, 25

Length 3,45 mm (holotype ♀). Head and pronotum black, elytra and venter reddish-brown, paler at mesosternum; antennae testaceous, darker at segments 7-11; legs reddish-brown. Microreticulation sometimes vague on head and pronotum, superficial on elytra; two sizes of impressed punctures on head and pronotum, superficial punctures on elytra.

Head: Widest behind eyes: temple $3/5$ length of eye (fig. 16); eyes convex; clypeus slightly excavated; clypeal line very shallow. Third antennal segment twice as long as 2nd, as 4th and 5th combined. Only traces of microreticulation; punctures of larger size impressed, spaced from each other by 3 times their own diameter; punctures of smaller size spaced from each other by 0,5-1 times their own diameter.

Pronotum: 1,44 times as broad as head, markedly broader than long ($W/L = 2$), little convex ($W/H = 2,05$). Dorsal and lateral outlines: fig. 17. Traces of microreticulation on entire surface; puncturation sparser than at head; two sizes of punctures. Holotype: length 0,88 mm, width 1,76 mm, height 0,87 mm.

Elytra: Moderately broader than pronotum, slightly broader than long ($W/L = 1,07$), moderately convex ($W/H = 1,59$); lateral outline with sharp humeral angle; sutural striae impressed, extending beyond the apical half of elytra. Punctures large, superficial, spaced from each other by 1-2 times their own diameter. Holotype: length 0,88 mm, width 1,83 mm, height 1,15 mm.

Metathoracic wings absent. Meso- and metasternum: median carina absent, lateral lines complete, femoral lines absent.

Legs: Tarsal formula: ♂ not known, ♀ 4-4-4.

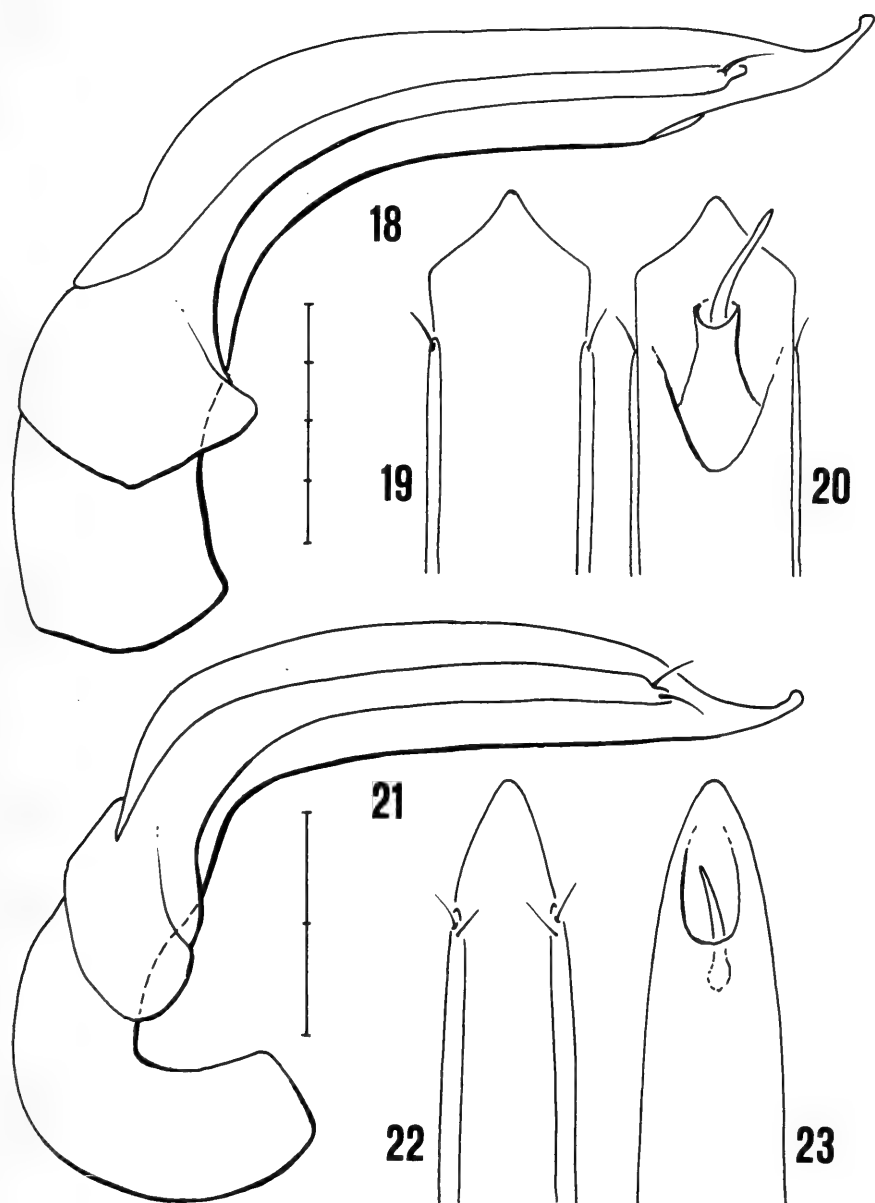
Spermatheca (fig. 25): Basal part elongate, twisted at duct connection; apical part stout, shorter.

HOLOTYPE ♀: Taichung Hsien, Hsuehshan, above Shan-Liu Gieu Hut, 3200 m, 8.V.1991, in MHNG.

Discussion: See the discussion of *A.yushanicum*. *Agathidium inquisitor* n.sp. is closely related to *A.geniculatum* n.sp., although these two species are different in size, ratio of 3rd/2nd antennal segments, coloration and puncturation of dorsum.

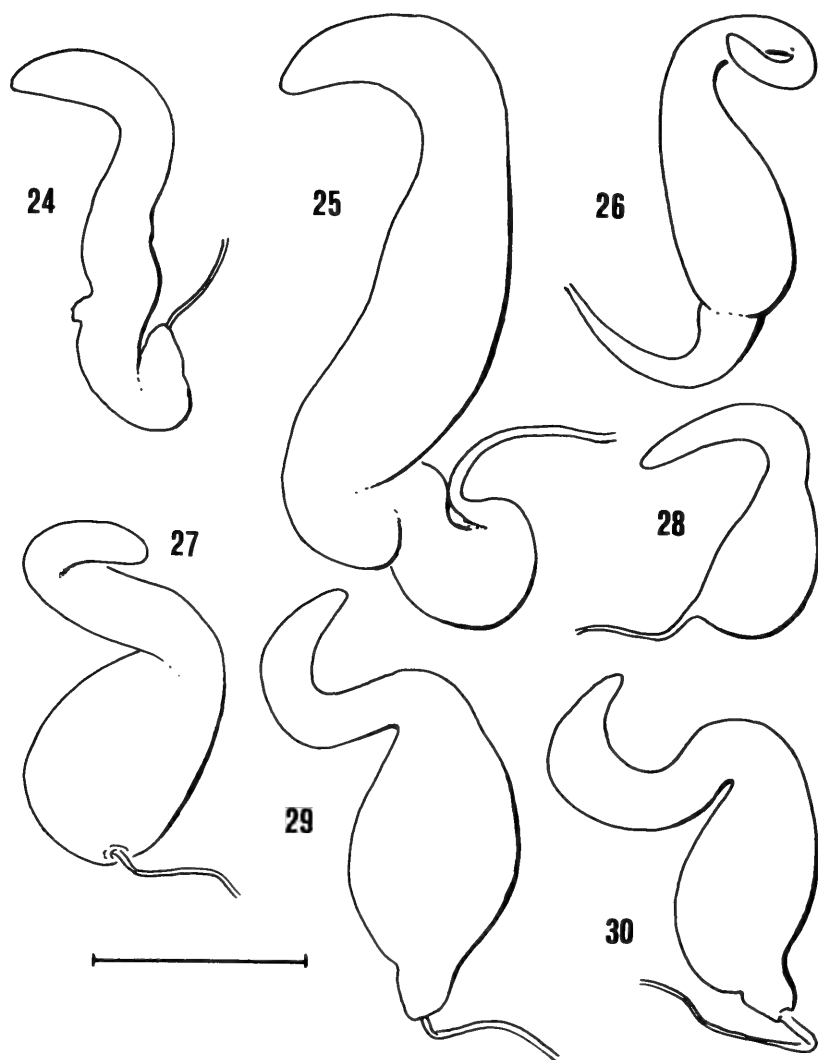
Habitat: Open *Abies* forest, dead leaves, rotting bark, wood and moss.

Distribution: Taiwan.



FIGS 18-23

Male copulatory organ (lateral view and dorsal/ventral view of its apex) of: 18-20, *Agathidium yushanicum* n.sp.; 21-23, *A. geniculatum* n.sp. Scales: 1 division = 0,1 mm.



FIGS 24-30

Spermatheca of: 24, *Agathidium yushanicum* n.sp.; 25, *A. inquisitor* n.sp.; 26, *A. geniculatum* n.sp.; 27, *A. praeustum* n.sp.; 28, *A. tarokoense* n.sp.; 29, *A. vestitum* n.sp.; 30, *A. rufomarginatum* n.sp. Scale: 1 division = 0,1 mm.

Agathidium (Cyphocele) geniculatum n.sp.

Figs. 21-23, 26

Length 2,5-2,8 mm (holotype ♂ 2,55 mm). Entire dorsum and venter reddish-brown, paler at mesosternum; antennae uniformly testaceous; legs reddish-brown. Microreticulation superficial or vague; puncturation dense on head, sparse on pronotum and elytra.

Head: Widest behind eyes; temple 1/2 length of eye; eyes flattened; clypeus slightly excavated; clypeal line very weak. Third antennal segment 1,8 times as long as 2nd, longer than 4th and 5th combined. Microreticulation very superficial or vague; punctures small, superficial, spaced from each other by 1-4 times their own diameter.

Pronotum: 1,45 times as broad as head, markedly broader than long (W/L = 1,84), moderately convex (W/H = 1,72). Microreticulation superficial, uniform; punctures as small as those on head, superficial, spaced from each other by 3-8 times their own diameter. Holotype: length 0,75 mm, width 1,38 mm, height 0,80 mm.

Elytra: Moderately narrower than pronotum, slightly broader than long (W/L = 1,08), moderately convex (W/H = 1,56); lateral outline with sharp humeral angle; sutural striae weak, confined to apical fifth of elytra. Only traces of microreticulation; punctures small, superficial, spaced from each other by 2-10 times their own diameter. Holotype: length 1,15 mm, width 1,25 mm, height 0,80 mm.

Metathoracic wings absent. Meso- and metasternum: median carina absent, lateral lines complete, femoral lines absent.

Legs: Tarsal formula: ♂ 5-5-4, ♀ 4-4-4; male tarsi slightly larger than those of females.

Male copulatory organ (figs 21-23): Aedeagus slender, with proximal part hook-like and apex bent up, lateral margins gently converging toward rounded apex, ventral piece indistinct; short endophallic flagellum protruding. Parameres slender, not enlarged at apex.

Spermatheca (fig. 26): Both basal and apical parts elongate; apical part twisted.

HOLOTYPE ♂: Nantou Hsien, Yushan N. P., Mun-Li Cliff, 2700 m, 13.V.1991, in MHNG.

PARATYPES: Together with the holotype, 2 ♀ in MHNG, 2 ♀ in NMNT; same locality, SW slope below Yushan Mn. peak, 3650 m, 14.V.1991, 1 ♀ in MHNG; Meifeng, 2130 m, 3.V.1991, 1 ♀ in MHNG; Taichung Hsien, Anmashan, 2225 m, 1.V.1990, 1 ♀ in MHNG, 1 ♀ in AC; same locality, 2225 m, 2.V.1990, 1 ♂ and 1 ♀ in AC; same locality, 2225 m, 3.V.1990, 1 ♂ in MHNG; same locality, 2230 m, 4.V.1990, 1 ♂ in MHNG; Hsuehshan, above Shan-Liu Gieu Hut, 3220 m, 7.V.1991, 1 ♂ in MHNG.

Discussion: See the discussion of *A. yushanicum* and *A. inquisitor*.

Habitat: Original broad-leaved forest, mouldy layers of fallen leaves and twigs around bases of large trees. Original *Abies* forest, rotting bark, wood and other plant debris. Subalpine zone, dense bushes of *Rhododendron*, with intermixed junipers.

Distribution: Taiwan.

Subg. **Neoceble** Gozis, 1886

Group: **nigripenne**

Agathidium (Neocele) praeustum n.sp.

Figs. 27, 31

Length 3,3 mm (holotype ♀). Entire dorsum and venter reddish-brown, paler at mesosternum (not fully sclerotized specimen); antennae testaceous, darker at segments 7-11; legs reddish-brown. Microreticulation vague, due to incomplete sclerotization; puncturation impressed on entire dorsum.

Head: Widest at eyes (fig. 31); eyes convex; clypeus moderately excavated; clypeal line very weak. Third antennal segment 1,6 times as long as 2nd, shorter than 4th and 5th combined; Hamann's organ: gutter with one vesicle in both 9th and 10th antennal segments. Microreticulation absent or vague; punctures moderately large, superficial, spaced from each other by 1-3 times their own diameter.

Pronotum: 1,6 times as broad as head, markedly broader than long ($W/L = 2$), slightly convex ($W/H = 1,85$). Microreticulation vague or absent; punctures somewhat larger than at head, impressed, spaced from each other by 1-6 times their own diameter. Holotype: length 0,90 mm, width 1,80 mm, height 0,97 mm.

Elytra: As broad as pronotum, moderately broader than long ($W/L = 1,12$), moderately convex ($W/H = 1,57$); lateral outline with sharp humeral angle; sutural striae weak, confined to apical half of elytra. Only traces of microreticulation; punctures larger and deeper than those of pronotum, spaced from each other by 1-4 times their own diameter. Holotype: length 1,60 mm, width 1,80 mm, height 1,14 mm.

Metathoracic wings absent. Meso- and metasternum: median carina weak, lateral lines complete, femoral lines absent.

Legs: Tarsal formula: ♂ not known, ♀ 4-4-4.

Spermatheca (fig. 27): Basal part pyriform, apical part elongate, twisted.

HOLOTYPE ♀: Pingtung Hsien, Peitawushan, trail at 2000 m, 23.V.1991, in MHNG.

Discussion: From the other *Neocele* species from Taiwan, *Agathidium praeustum* n.sp. differs by its larger size; furthermore, it differs from *A. nigrocastaneum* n.sp. in puncturation and coloration, from *A. tarokoense* n.sp., *A. vestitum* n.sp. and *A. rufomarginatum* n.sp. in the ratio of 3rd/2nd antennal segments.

Habitat: Original broad-leaved forest, lush undergrowth along trail.

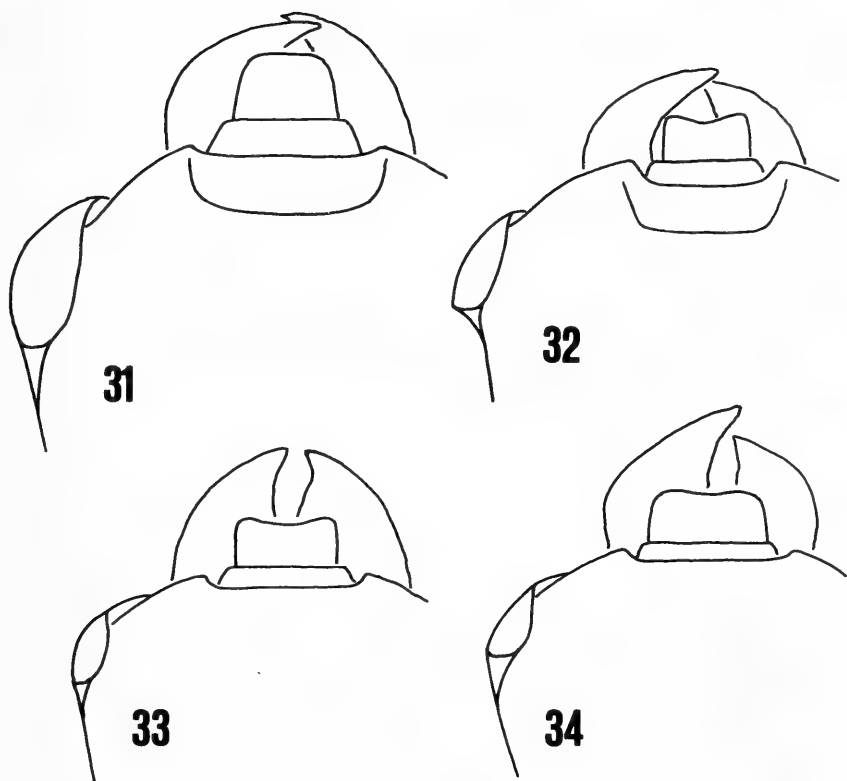
Distribution: Taiwan.

Agathidium (Neocele) nigrocastaneum n.sp.

Figs. 32, 35-37

Length 2,6-2,7 mm (holotype ♂ 2,60 mm). Head and pronotum black, elytra and venter reddish-brown, paler at mesosternum; antennae reddish-brown, darker at club; legs reddish-brown. Microreticulation absent, except for some traces on head and pronotum; puncturation fine, sparse on head and pronotum, absent on elytra.

Head: Widest at eyes (fig. 32); eyes convex; left mandible of males sometimes with a tooth (observed in the male paratype); clypeus much excavated; clypeal line absent. Third antennal segment 1,5 times as long as 2nd, as long as than 4th and 5th combined. Microreticulation absent; punctures small, superficial, spaced from each other by 4-10 times their own diameter.



FIGS 31-34

Head of: 31, *Agathidium praeustum* n.sp.; 32, *A. nigrocastaneum* n.sp.; 33, *A. vestitum* n.sp.; 34, *A. rufomarginatum* n.sp.

Pronotum: 1,40 times as broad as head, moderately broader than long ($W/L = 1,68$), moderately convex ($W/H = 1,72$). Only traces of microreticulation; punctures as small as those on head, sparser, spaced from each other by 5-20 times their own diameter. Holotype: length 0,82 mm, width 1,38 mm, height 0,80 mm.

Elytra: As broad as pronotum, moderately broader than long ($W/L = 1,15$), very convex ($W/H = 1,4$); lateral outline with sharp humeral angle; sutural striae weak, confined to apical half of elytra. Only traces of microreticulation; puncturation absent, except for some sparse, very small punctures. Holotype: length 1,20 mm, width 1,38 mm, height 0,98 mm.

Metathoracic wings present. Meso- and metasternum: median carina absent, lateral lines complete, femoral lines absent.

Legs: Tarsal formula: ♂ 5-5-4, ♀ 4-4-4; male tarsi slightly larger than those of females.

Male copulatory organ (figs 35-37): Aedeagus slender, with proximal part simple, lateral margins gently converging toward subacute apex, ventral piece slightly emarginate. Parameres slender, gently narrowing toward apex.

Spermatheca : not found in either of female paratypes.

HOLOTYPE ♂: Hualien Hsien, Taroko N. P., ridge SE Nanhushi Hut, 2700 m, 11.V.1990, in MHNG.

PARATYPES: Together with the holotype, 2 ♀ in AC; same locality, Nanhushi Hut, 2220 m, 8.V.1990, 1 ♂ in NMNT.

Discussion: See the discussion of *A. praeustum*. *Agathidium nigrocastaneum* n.sp. differs from *A. tarokoense* n.sp., *A. vestitum* n.sp. and *A. rufomarginatum* n.sp. in the ratio of 3rd/2nd antennal segments and in the size and coloration of antennae.

Habitat: Original coniferous forest, rotting bark and wood, humus, moss and old mushrooms on and around fallen trees.

Distribution: Taiwan.

Group: **marginatum**

Agathidium (Neoceleble) tarokoense n.sp.

Figs. 28, 38-40

Length 2,1-2,3 mm (holotype ♂ 2,30 mm). Dorsum black, reddish at elytra apex; venter black, reddish-brown at mesosternum; antennae testaceous, darker at club; legs reddish-brown. Entire dorsum with superficial microreticulation and with fine, sparse puncturation.

Head: Widest at the posterior margin of eyes; eyes convex; clypeus slightly excavated; clypeal line very weak. Third antennal segment 0,7 times as long as 2nd, shorter than 4th and 5th combined. Microreticulation superficial, uniform; punctures small, superficial, spaced from each other by 2-10 times their own diameter.

Pronotum: 1,6 times as broad as head, moderately broader than long (W/L = 1,66), moderately convex (W/H = 1,60). Microreticulation superficial; punctures as small as those on head, sparser. Holotype: length 0,72 mm, width 1,20 mm, height 0,75 mm.

Elytra: Slightly narrower than pronotum, moderately broader than long (W/L = 1,1), very convex (W/H = 1,41); lateral outline with sharp humeral angle; sutural striae absent. Microreticulation superficial; punctures larger than at head, superficial, spaced from each other by 1-10 times their own diameter. Holotype: length 1,05 mm, width 1,16 mm, height 0,82 mm.

Metathoracic wings present. Meso- and metasternum: median carina absent, lateral lines complete, femoral lines absent.

Legs: Tarsal formula: ♂ 4-4-4, ♀ 4-4-4; male tarsi slightly larger than those of females.

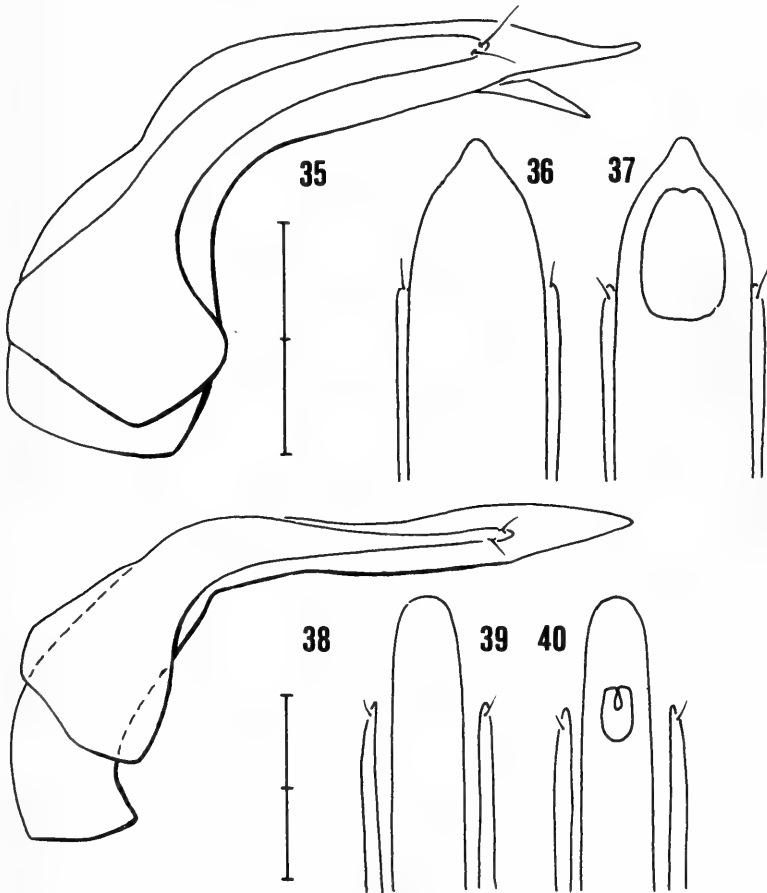
Male copulatory organ (figs 38-40): Aedeagus slender, with proximal part simple, lateral margins parallel, apex broadly rounded, ventral piece bifid. Parameres slender, slightly enlarged at apex.

Spermatheca (fig. 28): Basal part pyriform, apical part elongate.

HOLOTYPE ♂: Hualien Hsien, Taroko N. P., ridge SE Nanhushi Hut, 2700 m, 11.V.1990, in MHNG.

PARATYPES: Together with the holotype, 1 ♀ in NMNT; Nantou Hsien, Yushan N. P., Pai-Yun Hut, 2 Km W Pai-Yun Hut, 3375 m, 17.V.1991, 2 ♂ in AC.

Discussion: See the discussion of *A. praeustum* and *A. nigrocastaneum*; *Agathidium tarokoense* n.sp. differs from *A. vestitum* n.sp. and *A. rufomarginatum* n.sp. by the ratio of 3rd/2nd antennal segments, by the presence of traces of micro-reticulation, by the coloration of dorsum and antennae and the pronotum/head width ratio.



FIGS 35-40

Male copulatory organ (lateral view and dorsal/ventral view of its apex) of: 35-37, *Agathidium nigrocastaneum* n.sp.; 38-40, *A. tarokoense* n.sp. Scales: 1 division = 0,1 mm.

Habitats: Original *Abies* forest, rotting bark and wood along fallen trees. Original coniferous forest, rotting bark and wood, humus, moss and old mushrooms on and around fallen trees.

Distribution: Taiwan.

Group: **canariense**

Agathidium (Neoceleble) vestitum n.sp.

Figs. 29, 33, 41-43

Length 2,1-2,5 mm (holotype ♂ 2,10 mm). Entire dorsum and venter dark reddish-brown; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on entire dorsum, except for some traces on elytra; puncturation very sparse on head, pronotum and elytra, deeper on elytra.

Head: Widest at eyes (fig. 33); eyes convex; clypeus moderately excavated; clypeal line absent. Third antennal segment as long as 2nd, shorter than 4th and 5th combined; Hamann's organ: gutter without vesicle in both 9th and 10th antennal segments. Microreticulation absent; punctures very small, superficial, spaced from each other by 2-10 times their own diameter.

Pronotum: 1,32 times as broad as head, markedly broader than long ($W/L = 1,98$), moderately convex ($W/H = 1,64$). Punctures as small as those on head, sparser, spaced from each other by 2-15 times their own diameter. Holotype: length 0,58 mm, width 1,15 mm, height 0,70 mm.

Elytra: As broad as pronotum, moderately broader than long ($W/L = 1,27$), very convex ($W/H = 1,35$); lateral outline with broadly rounded humeral angle; sutural striae absent. Only traces of microreticulation; punctures moderately large, superficial, spaced from each other by 3-6 times their own diameter. Holotype: length 0,90 mm, width 1,15 mm, height 0,85 mm.

Metathoracic wings absent. Meso- and metasternum: median carina weak, lateral lines absent, femoral lines absent.

Legs: Tarsal formula: ♂ 5-5-4, ♀ 5-4-4; male tarsi not larger than those of females.

Male copulatory organ (figs 41-43): Aedeagus slender, with proximal part simple and apex bent up, lateral margins parallel and then abruptly converging toward rounded apex, ventral piece indistinct. Parameres slender, slightly enlarged at apex.

Spermatheca (fig. 29): Basal part pyriform, apical part elongate, twisted.

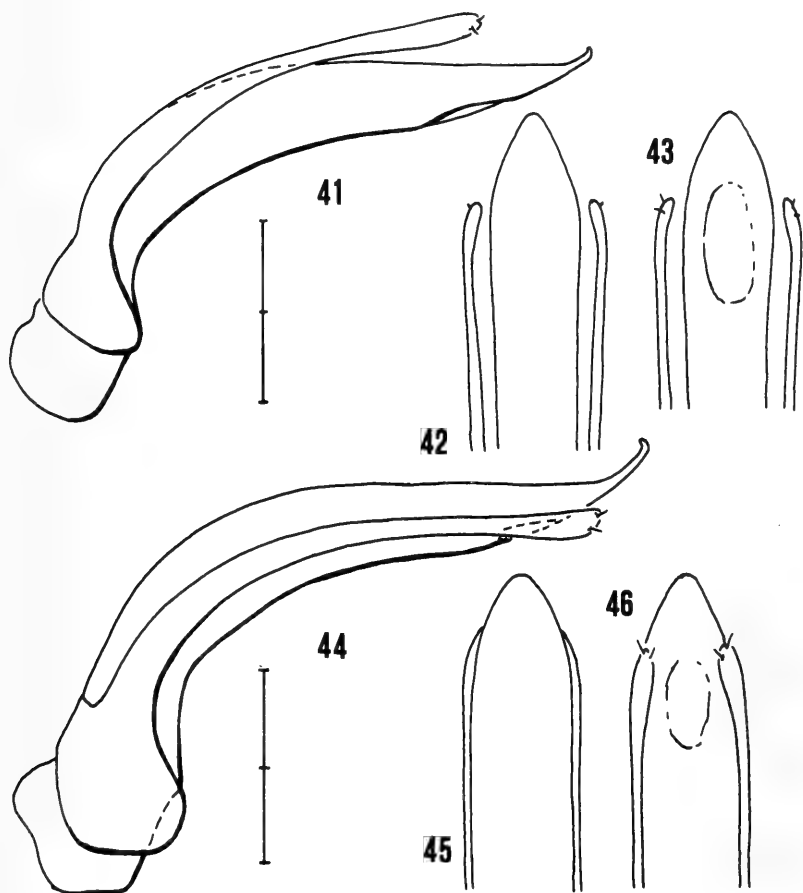
HOLOTYPE ♂: Pingtung Hsien, Peitawushan, trail at 2000 m, 23.V.1991, in MHNG.

PARATYPE: Together with the holotype, 1 ♀ in AC.

Discussion: See the discussion of *A. tarokoense*. *Agathidium vestitum* n.sp. differs from *A. rufomarginatum* n.sp. by the shape of head, the coloration of antennae, by the female tarsal formula and by the deeper elytral puncturation.

Habitat: Original broad-leaved forest, lush undergrowth along a trail, plant debris and litter.

Distribution: Taiwan.



FIGS 41-46

Male copulatory organ (lateral view and dorsal/ventral view of its apex) of: 41-43, *Agathidium vestitum* n.sp.; 44-46, *A. rufomarginatum* n.sp. Scales: 1 division = 0,1 mm.

***Agathidium (Neocele) rufomarginatum* n.sp.**

Figs. 30, 34, 44-46

Length 2,2-2,5 mm (holotype ♂ 2,50 mm). Entire dorsum dark reddish-brown, paler at sides; venter reddish-brown; antennae testaceous, darker at segments 9-10; legs reddish-brown. Microreticulation absent on entire dorsum; puncturation very sparse on entire dorsum.

Head: Widest at eyes (fig. 34); eyes convex; clypeus slightly excavated; clypeal line absent. Third antennal segment as long as 2nd, shorter than 4th and 5th combined. Punctures very small, superficial, hardly visible.

Pronotum: 1,37 times as broad as head, moderately broader than long ($W/L = 1,72$), moderately convex ($W/H = 1,65$). Punctures very small, superficial, hardly visible. Holotype: length 0,72 mm, width 1,24 mm, height 0,75 mm.

Elytra: As broad as pronotum, moderately broader than long ($W/L = 1,09$), very convex ($W/H = 1,41$); lateral outline with sharp humeral angle; sutural striae absent. Punctures very small, as on head. Holotype: length 1,10 mm, width 1,20 mm, height 0,85 mm.

Metathoracic wings absent. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines absent.

Legs: Tarsal formula: ♂ 5-5-4, ♀ 4-4-4; male tarsi slightly larger than those of females.

Male copulatory organ (figs 44-46): Aedeagus slender, with proximal part simple and apex bent up, lateral margins parallel and then abruptly converging toward broadly rounded apex, ventral piece indistinct. Parameres slender, slightly enlarged at apex.

Spermatheca (fig. 30): Basal part pyriform, with tubercle at duct connection; apical part elongate, twisted.

HOLOTYPE ♂: Hualien Hsien, Taroko N. P., ridge SE Nanhushi Hut, 2700 m, 11.V.1990, in MHNG.

PARATYPE: Together with the holotype, 1 ♀ in AC.

Discussion: See the discussion of *A. vestitum*.

Habitat: Original coniferous forest, rotting bark and wood, humus, moss and old mushrooms on and around fallen trees.

Distribution: Taiwan.

Subg. **Macroceble** Angelini, 1993

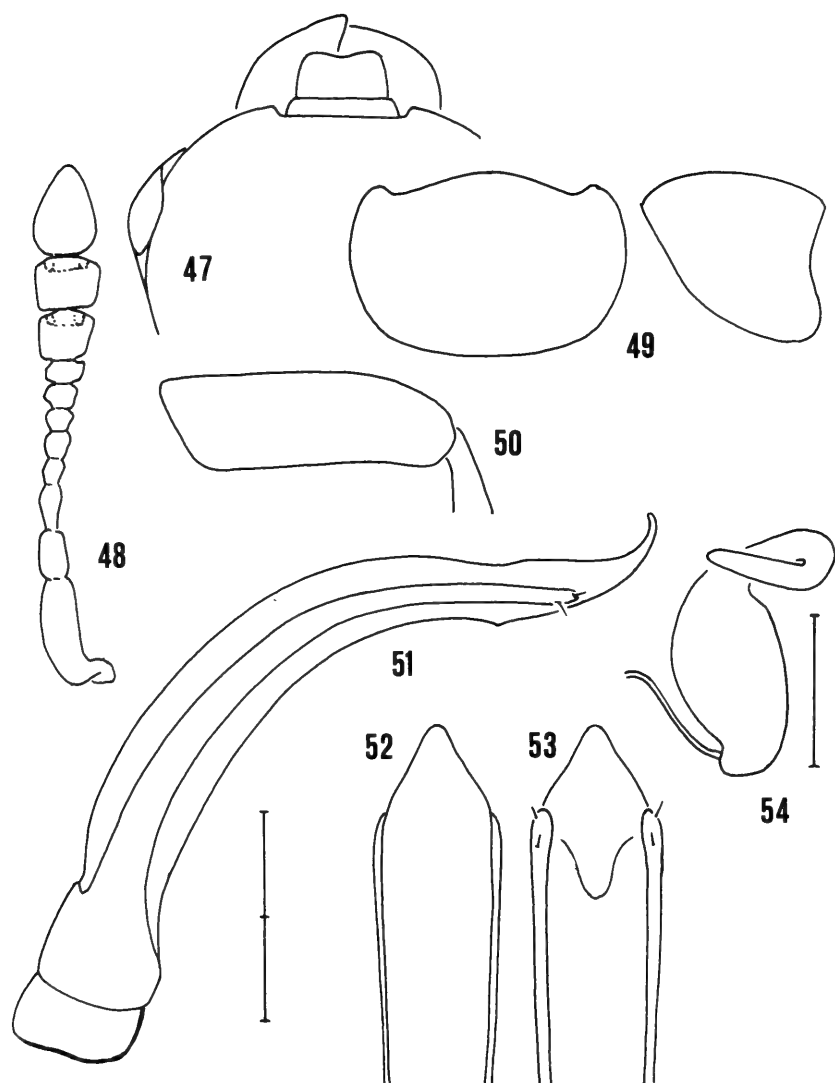
Agathidium (Macroceble) oblitum n.sp.

Figs. 47-54

Length 2,3-2,4 mm (holotype ♂ 2,40 mm). Entire dorsum dark reddish-brown or black; venter reddish-brown; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on entire dorsum; puncturation very sparse on entire dorsum.

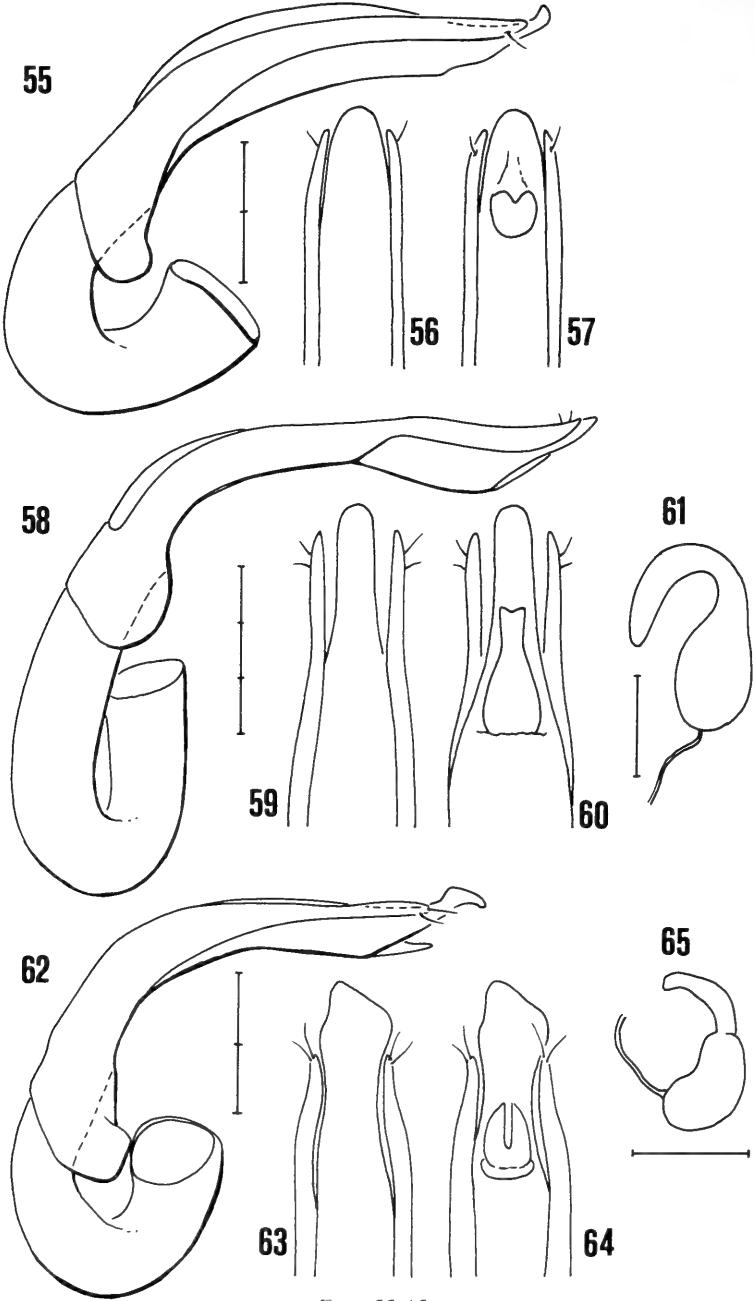
Head: Widest at eyes (fig. 47); eyes convex; clypeus slightly excavated; clypeal line absent; antero-lateral margins raised; left male mandible sometimes with a strong tooth. Third antennal segment as long as 2nd, shorter than 4th and 5th combined (fig. 48); Hamann's organ: gutter without vesicle in both 9th and 10th antennal segments. Punctures very small, impressed, spaced from each other by 1-6 times their own diameter.

Pronotum: 1,28 times as broad as head, moderately broader than long ($W/L = 1,51$), moderately convex ($W/H = 1,57$). Dorsal and lateral outlines: fig. 49. Punctures as small as those on head, superficial, spaced from each other by 1-20 times their own diameter. Holotype: length 0,74 mm, width 1,12 mm, height 0,71 mm.



FIGS 47-54

Agathidium oblitum n.sp.: head, antenna, pronotum (dorsal and lateral outline) male hind femur, male copulatory organ (lateral view and dorsal/ventral view of its apex) and spermatheca. Scales: 1 division = 0,1 mm.



FIGS. 55-65

Male copulatory organ (lateral view and dorsal/ventral view of its apex) and spermatheca of: 55-57, *Agathidium tardum* n.sp.; 58-61, *A. distinguendum* n.sp.; 62-65, *A. familiare* n.sp. Scales: 1 division = 0,1 mm.

Elytra: As broad as pronotum, as broad as long, moderately convex ($W/H = 1.54$); lateral outline with broadly rounded humeral angle; sutural striae absent. Punctures as small as those of pronotum, superficial. Holotype: length 1.09 mm, width 1.08 mm, height 0.70 mm.

Metathoracic wings absent. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines indistinct due to extremely abbreviated metasternum; a small tubercle between metacoxae.

Legs: Tarsal formula: ♂ 5-5-4, ♀ 4-4-4; male tarsi not larger than those of females (fig. 50).

Male copulatory organ (figs 51-53): Aedeagus very slender, with proximal part simple and apex bent up, lateral margins parallel and then abruptly converging toward rounded apex, ventral piece indistinct. Parameres slender, gently narrowing toward apex.

Spermatheca (fig. 54): Basal part pyriform, apical part elongate, twisted.

HOLOTYPE ♂: Kaohsiung Hsien, Tengchih, 1610 m, 24.IV.1990, in MHNG.

PARATYPES: Together with the holotype, 2 ♂ in MHNG, 1 ♂ in NMNT, 1 ♂ and 1 ♀ in AC; same locality, 1535 m, 23.IV.1990, 1 ♀ in MHNG; Taichung Hsien, Anmashan, 2225 m, 1.V.1990, 1 ♀ in MHNG; same locality, 2230 m, 4.V.1990, 1 ♀ in MHNG; Nantou Hsien, Shanlinchi, 1650 m, 16.IV.1990, 1 ♂ in MHNG; Meifeng, 2130, 12.V.1991, 1 ♂ in AC; Chiai Hsien, Yushan N. P., Mun-Li Cliff, 1700 m, 27.IV.1990, 1 ♀ in MHNG.

Discussion: *Agathidium oblitum* n.sp. may be easily separated on the base of the key to species; when compared with the other *Macroceble* species, it is closely related to *A. fulcratum* Ang. & Dmz. (1994: 41, Nepal) and *A. jaccoudi* Ang. & Dmz. (1986a: 429, Malaya), but it differs from both by the presence of the mesosternal carina, and by the shape of the aedeagus; it also differs from the latter species also by the female tarsal formula.

Habitats: Coniferous forest of *Taiwania cryptomeroides*. Large clearing in a broad-leaved forest. Original broad-leaved forest, plant debris and humus under fallen trees. Original mixed coniferous and broad-leaved forest.

Distribution: Taiwan.

Subg. **Agathidium** s.str. Panzer, 1797

Group: **madurensis**

Agathidium (s.str.) **tardum** n.sp.

Figs. 55-57

Length 2.75 mm (holotype ♂). Entire dorsum reddish-brown; antennae testaceous, darker at club; legs reddish-brown. Microreticulation absent on entire dorsum, except for some traces on elytra; puncturation fine and sparse on entire dorsum.

Head: Widest at eyes; eyes convex; clypeus moderately excavated; clypeal line absent; antero-lateral margins raised. Third antennal segment 1.8 times as long as 2nd, longer than 4th and 5th combined. Punctures small, superficial, spaced from each other by 3-10 times their own diameter.

Pronotum: 1,66 times as broad as head, moderately broader than long ($W/L = 1,56$), very convex ($W/H = 1,44$). Punctuation as that of head. Holotype: length 0,83 mm, width 1,30 mm, height 0,90 mm.

Elytra: Slightly narrower than pronotum, as broad as long, moderately convex ($W/H = 1,78$); lateral outline with broadly rounded humeral angle; sutural striae absent. Only traces of microreticulation; punctures twice as broad as those on head, spaced from each other by 1-10 times their own diameter. Holotype: length 1,25 mm, width 1,25 mm, height 0,97 mm.

Metathoracic wings present. Meso- and metasternum: median carina weak, lateral lines absent, femoral lines incomplete.

Legs: Male hind femora broadened distally. Tarsal formula: ♂ 5-5-4, ♀ not known.

Male copulatory organ (figs 55-57): Aedeagus very slender, with proximal part hook-like and apex bent up, lateral margins parallel, apex broadly rounded, ventral piece deeply emarginate. Parameres slender, gently narrowing toward apex.

HOLOTYPE ♂: Kaohsiung Hsien, Tengchih, 1610 m, 24.IV.1990, in MHNG.

Discussion: *Agathidium tardum* n.sp. clearly differs from the other Taiwanese species of the *madurensis* group by the ratio of 3rd/2nd antennal segments and by the coloration of the antennal club; furthermore, it differs from *A. distinguendum* n.sp. by the possession of the metathoracic wings and by the pronotum/head ratio.

Habitat: Large clearing in a broad-leaved forest, dead vegetation and humus, rotting bark and wood along fallen trees and stumps.

Distribution: Taiwan.

***Agathidium* (s.str.) *distinguendum* n.sp.**

Figs. 58-61

Length 3,0-3,7 mm (holotype ♂ 3,65 mm). Entire dorsum black; venter reddish-brown, paler at mesosternum; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on entire dorsum; punctuation very sparse on head and pronotum, absent on elytra.

Head: Widest at eyes; eyes convex; clypeus sharply excavated; clypeal line absent; antero-lateral margins not raised. Third antennal segment 1,2 times as long as 2nd, as long as 4th and 5th combined. Punctures very small, superficial, hardly visible.

Pronotum: 1,45 times as broad as head, slightly broader than long ($W/L = 1,35$), very convex ($W/H = 1,3$). Punctures as small and sparse as those on head. Holotype: length 1,35 mm, width 1,70 mm, height 0,30 mm.

Elytra: Slightly narrower than pronotum, as broad as long, moderately convex ($W/H = 1,53$); lateral outline with broadly rounded humeral angle; sutural striae absent. Holotype: length 1,55 mm, width 1,47 mm, height 0,96 mm.

Metathoracic wings absent. Meso- and metasternum: median carina weak, lateral lines absent, femoral lines complete.

Legs: Male hind femora with a very large tooth. Tarsal formula: ♂ 5-5-4, ♀ 5-4-4.

Male copulatory organ (figs 58-60): Aedeagus very slender, with ring-like proximal part, lateral margins gently converging toward rounded apex, ventral piece slightly emarginate. Parameres stout, abruptly narrowed at middle of their length.

Spermatheca (fig. 61): Basal part pyriform, apical part elongate.

HOLOTYPE ♂: Kaohsiung Hsien, Tengchih, 1580 m, 24.IV.1990, in MHNG.

PARATYPES: Together with the holotype, 2 ♂ in MHNG, 1 ♂ in NMNT, 1 ♀ in AC; same locality, 1535 m, 23.IV.1990, 1 ♂ in MHNG, 1 ♂ in NMNT, 2 ♂ in AC; same locality, 1610 m, 24.IV.1990, 2 ♂ in MHNG.

Discussion: See the discussion of *A. tardum*. *Agathidium distinguendum* n.sp. differs from *A. formosum* Ang. & Dmz. (1985: 32, Taiwan) and *A. familiare* n.sp. by the coloration of the dorsum and the antennae, and by the shape of the male hind femora; furthermore, it differs from the former by the absence of the metathoracic wings and from the latter by the absence of the puncturation and traces of microreticulation on the elytra.

Habitats: Coniferous forest of *Taiwanis cryptomeroides*. Large clearing in a broad-leaved forest, dead vegetation and humus, rotting bark and wood along fallen trees and stumps.

Distribution: Taiwan.

***Agathidium* (s.str.) *familare* n.sp.**

Figs. 62-65

Length 2,5-2,7 mm (holotype ♂ 2,65 mm). Entire dorsum and venter reddish-brown, paler at mesosternum; antennae testaceous, darker at segments 7-11; legs reddish-brown. Microreticulation absent on entire dorsum, except for some traces on elytra; puncturation fine and sparse on entire dorsum.

Head: Widest at eyes; eyes convex; clypeus moderately excavated; clypeal line absent; antero-lateral margins raised. Third antennal segment as long as 2nd, shorter than 4th and 5th combined. Punctures small, superficial, spaced from each other by 1-8 times their own diameter.

Pronotum: 1,44 times as broad as head, moderately broader than long ($W/L = 1,51$), very convex ($W/H = 1,44$). Puncturation as that of head. Holotype: length 0,86 mm, width 1,30 mm, height 0,90 mm.

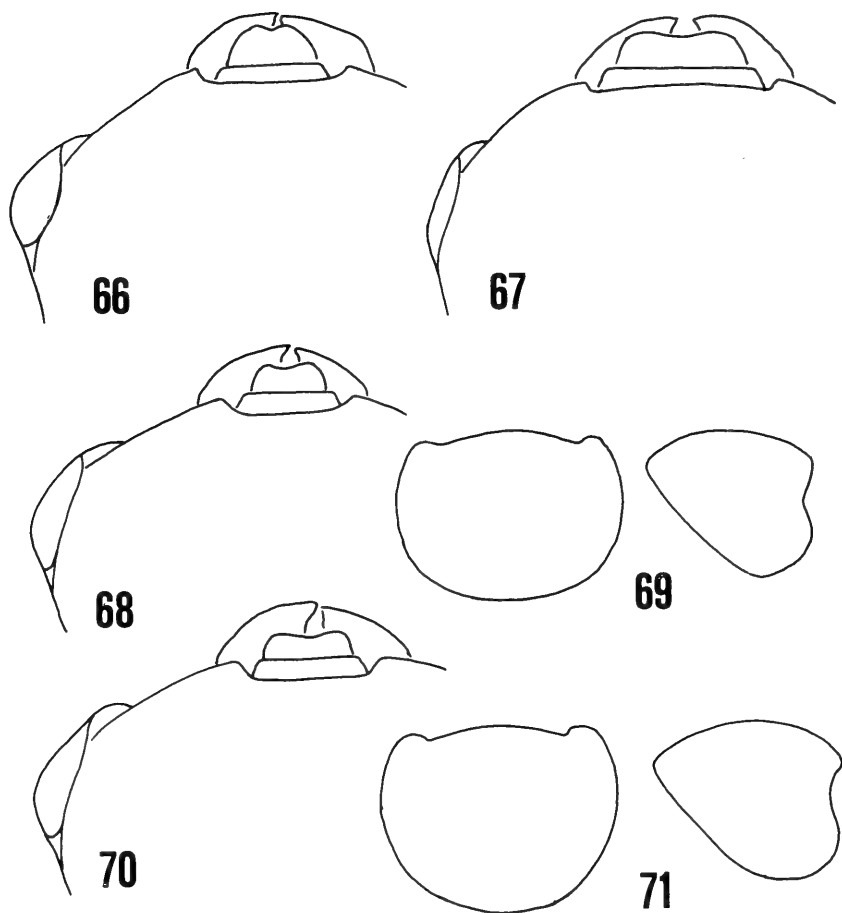
Elytra: Slightly narrower than pronotum, nearly as broad as long ($W/L = 1,08$), slightly convex ($W/H = 1,86$); lateral outline with broadly rounded humeral angle; sutural striae absent. Only traces of microreticulation; punctures very small, superficial, spaced from each other by 5-15 times their own diameter. Holotype: length 1,15 mm, width 1,25 mm, height 0,67 mm.

Metathoracic wings absent. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines incomplete.

Legs: Male hind femora broadened distally. Tarsal formula: ♂ 5-5-4, ♀ 5-4-4.

Male copulatory organ (figs 62-64): Aedeagus slender, with proximal part hook-like and apex bent up, lateral margins sinuate, apex asymmetrical, subacute, ventral piece deeply bifid. Parameres slender, gently narrowing toward apex.

Spermatheca (fig. 65): Basal part pyriform, apical part elongate.

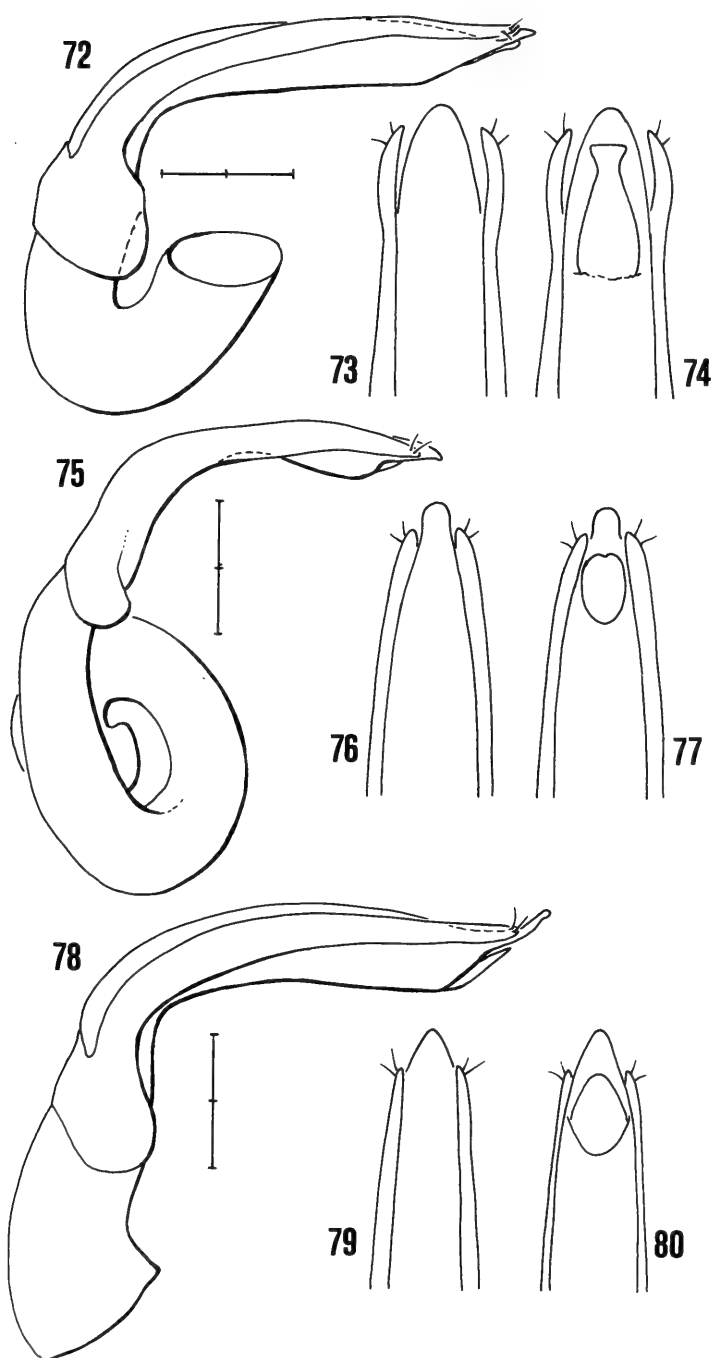


FIGS 66-71

Pronotum (dorsal and lateral outline) and/or head of: 66, *Agathidium lucidum* n.sp.; 67, *A. tenebroides* n.sp.; 68-69, *A. tessellatum* n.sp.; 70-71, *A. memnonium* n.sp.

FIGS 72-80

Male copulatory organ (lateral view and dorsal/ventral view of its apex) of: 72-74, *Agathidium glabricolle* n.sp.; 75-77, *A. honestum* n.sp.; 78-80, *A. lucidum* n.sp. Scales: 1 division = 0,1 mm.



HOLOTYPE ♂: Chiai Hsien, Yushan N. P., Mun-Li Cliff, 1700 m, 27.IV.1990, in MHNG.

PARATYPES: Together with the holotype, 2 ♀ in MHNG, 1 ♂ and 1 ♀ in NMNT, 1 ♂ in AC; Taichung Hsien, Anmashan, 2225 m, 2.V.1990, 1 ♂ in MHNG; Taoyuan Hsien, Takuanshan For., 1650 m, 17.IV.1990, 1 ♀ in MHNG, 1 ♂ in AC; Nantou Hsien, Shanlinchi, 1650 m, 16.IV.1990, 1 ♀ in MHNG; Yushan N. P., Mun-Li Cliff, 2700 m, 18.V.1991, 1 ♂ in MHNG; Kaohsiung-Hsien, Tengchih, 1610 m, 24.IV.1990, 1 ♀ in MHNG, 1 ♀ in AC.

Discussion: See the discussion of *A. distinguendum*.

Habitats: Large clearing in a broad-leaved forest, dead vegetation and humus, rotting bark and wood along fallen trees and stumps. Original broad-leaved forest. Original mixed coniferous and broad-leaved forest.

Distribution: Taiwan.

Group: **seminulum**

Agathidium (s.str.) glabricolle n.sp.

Figs. 72-74, 94, 113

Length 2,9-3,0 mm (holotype ♂ 3,05 mm). Entire dorsum reddish-brown; antennae testaceous, darker at segments 9-10; legs reddish-brown. Microreticulation absent on entire dorsum, except for some traces on elytra; punctures very small on entire dorsum.

Head: Widest just a little behind eyes; eyes flattened; clypeus moderately excavated; clypeal line absent; antero-lateral margins not raised. Third antennal segment 1,6 times as long as 2nd, as long as 4th and 5th combined. Punctures small, superficial, spaced from each other by 6-10 times their own diameter.

Pronotum: 1,45 times as broad as head, moderately broader than long ($W/L = 1,45$), very convex ($W/H = 1,47$). Punctuation as that of head. Holotype: length 0,96 mm, width 1,40 mm, height 0,95 mm.

Elytra: As broad as pronotum, as broad as long, moderately convex ($W/H = 1,62$); lateral outline with broadly rounded humeral angle; sutural striae absent. Only traces of microreticulation; punctures as small as those of pronotum, sparser. Holotype: length 1,36 mm, width 1,40 mm, height 0,86 mm.

Metathoracic wings absent. Meso- and metasternum: median carina weak absent, lateral lines absent, femoral lines complete.

Legs: Male hind femora with a small distal tooth (fig. 94). Tarsal formula: ♂ 5-5-4, ♀ 5-4-4.

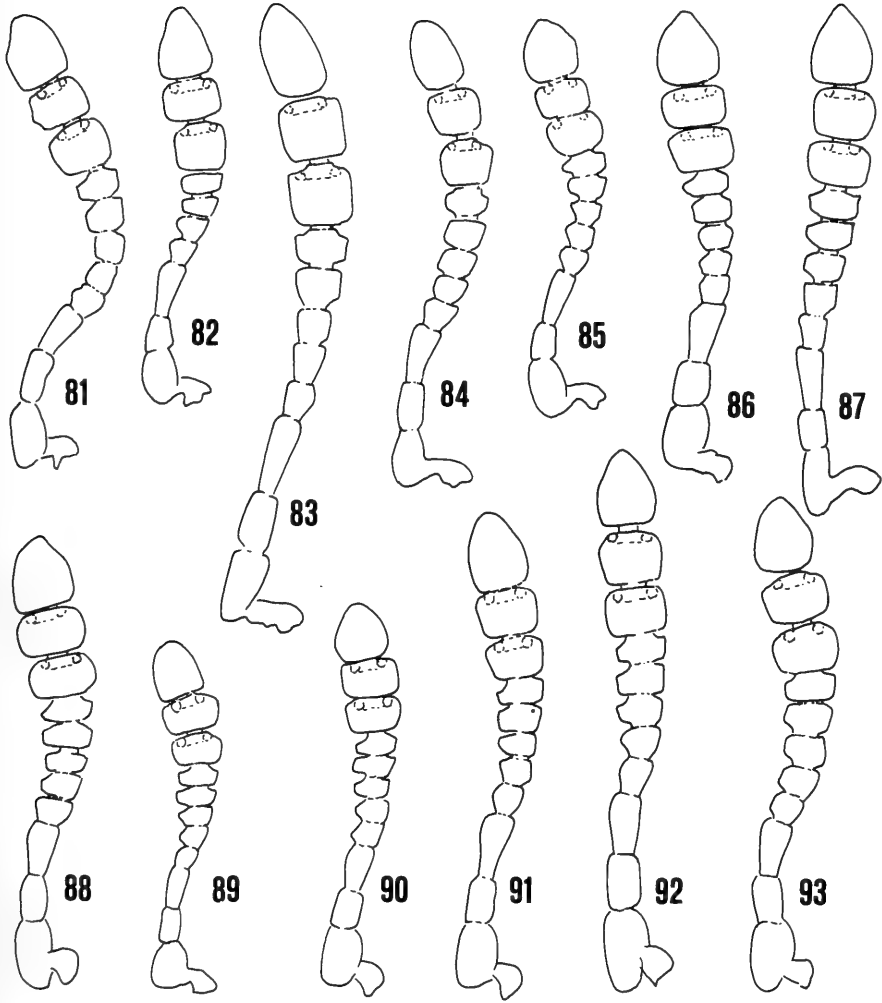
Male copulatory organ (figs 72-74): Aedeagus very slender, with proximal part hook-like, lateral margins gently converging toward broadly rounded apex, ventral piece not bifid. Parameres slender, gently narrowing toward apex.

Spermatheca (fig. 113): Basal part pyriform, apical part elongate.

HOLOTYPE ♂: Taichung Hsien, Anmashan, 2230 m, 4.V.1990, in MHNG.

PARATYPES: Nantou Hsien, Meifeng, 2130 m, 3.V.1991, 1 ♀ in MHNG, 1 ♀ in AC.

Discussion: *Agathidium glabricolle* n.sp. may be easily distinguished from any other species of *Agathidium* of Taiwan by the possession of sutural striae and microreticulation, which are characters of the *seminulum* group. Within SE Asia, the species of this group were previously known only from the Himalaya and Meghalaya.



FIGS. 81-93

Antenna of: 81, *Agathidium honestum* n.sp.; 82, *A. discretum* n.sp.; 83, *A. meifengense* n.sp.; 84, *A. kaohsiungense* n.sp.; 85, *A. chalconotum* n.sp.; 86, *A. angustatum* n.sp.; 87, *A. fuliginosum* n.sp.; 88, *A. alpestre* n.sp.; 89, *A. furcatum* n.sp.; 90, *A. comptum* n.sp.; 91, *A. intricatum* n.sp.; 92, *A. taichungense* n.sp.; 93, *A. exoletum* n.sp.

Habitat: Original broad-leaved forest, rotting bark, wood and other debris.
Distribution: Taiwan.

Group: **laevigatum**

Agathidium (s.str.) honestum n.sp.

Figs. 75-77, 81, 95

Length 2,8 mm (holotype ♂ 2,85 mm). Entire dorsum dark reddish-brown; venter reddish-brown; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on entire dorsum, except for some traces on elytra; punctures very small on entire dorsum.

Head: Widest at eyes; eyes convex; clypeus moderately excavated; clypeal line absent; antero-lateral margins not raised. Third antennal segment as long as 2nd, shorter than 4th and 5th combined (fig. 81); Hamann's organ: gutter without vesicle in both 9th and 10th antennal segments. Only some very small punctures.

Pronotum: 1,27 times as broad as head, slightly broader than long ($W/L = 1,27$), very convex ($W/H = 1,34$). Only some very small punctures. Holotype: length 1,02 mm, width 1,30 mm, height 0,97 mm.

Elytra: Slightly narrower than pronotum, slightly broader than long ($W/L = 1,08$), moderately convex ($W/H = 1,78$); lateral outline with broadly rounded humeral angle; sutural striae absent. Microreticulation very superficial; punctures sparse and very small. Holotype: length 1,15 mm, width 1,25 mm, height 0,70 mm.

Metathoracic wings absent. Meso- and metasternum: median carina absent, lateral lines absent, femoral lines complete.

Legs: Male hind femora with very sharp tooth (fig. 95). Tarsal formula: ♂ 5-5-4, ♀ not known.

Male copulatory organ (figs 75-77): Aedeagus very slender, with spiralled proximal part, lateral margins gently converging toward rounded apex, ventral piece not bifid. Parameres stout, gently narrowing toward apex.

HOLOTYPE ♂: Pingtung Hsien, Peitawushan, Kuai-Ku Hut, 2325 m, 21.V.1991, in MHNG.

PARATYPES: Together with the holotype, 1 ♂ in AC, 1 ♂ in NMNT.

Discussion: *Agathidium honestum* n.sp. is closely related to *A. lucidum* n.sp. and *A. tenebroides* n.sp. based on the length ratio of 3rd/2nd antennal segments, which is 1 or lower; it differs by the coloration of the dorsum, by the shape of the male hind femora and by the carinate mesosternum; furthermore, it differs from the former species by the width ratio of pronotum/head.

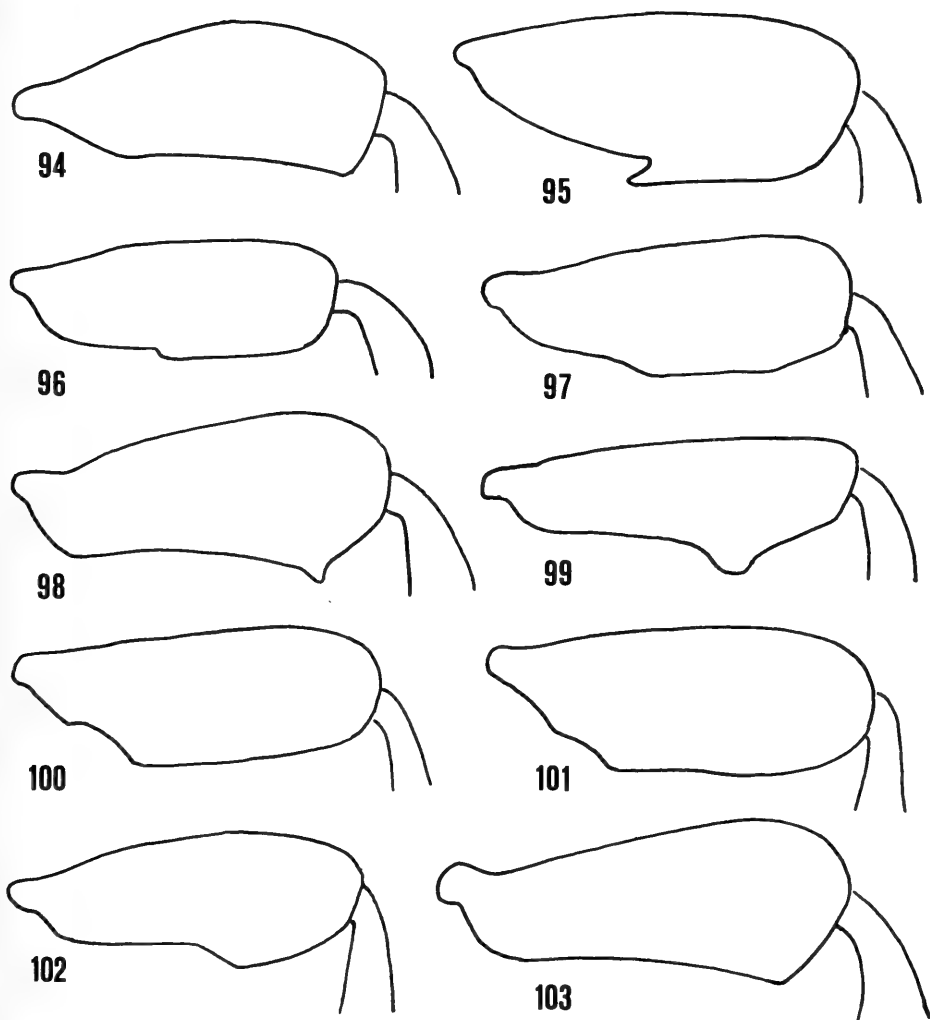
Habitat: Original broad-leaved forest, dead vegetation, fallen leaves and other debris.

Distribution: Taiwan.

Agathidium (s.str.) lucidum n.sp.

Figs. 66, 78-80, 96, 114

Length 2,6-2,9 mm (holotype ♂ 2,85 mm). Entire dorsum black; venter reddish-brown; antennae uniformly testaceous; legs reddish-brown. Microreticulation



FIGS 94-103

Male hind femur of: 94, *Agathidium glabricolle* n.sp.; 95, *A. honestum* n.sp.; 96, *A. lucidum* n.sp.; 97, *A. tenebroides* n.sp.; 98, *A. discretum* n.sp.; 99, *A. meifengense* n.sp.; 100, *A. tessellatum* n.sp.; 101, *A. memnonium* n.sp.; 102, *A. kaohsiungense* n.sp.; 103, *A. chalconotum* n.sp.

vague on head and pronotum; punctures very small on head and pronotum, absent on elytra.

Head: Punctures small, superficial, spaced from each other by 1-5 times their own diameter. Widest at eyes (fig. 66); eyes convex; clypeus moderately excavated; clypeal line absent; antero-lateral margins raised. Third antennal segment 0,9 times as long as 2nd, shorter than 4th and 5th combined. Only traces of microreticulation.

Pronotum: 1,47 times as broad as head, slightly broader than long ($W/L = 1,3$), moderately convex ($W/H = 1,52$). Only traces of microreticulation; punctures as small as those on head, sparser. Holotype: length 1,00 mm, width 1,30 mm, height 0,85 mm.

Elytra: Slightly narrower than pronotum, as broad as long, slightly convex ($W/H = 1,87$); lateral outline with broadly rounded humeral angle; sutural striae absent. Only traces of microreticulation. Holotype: length 1,20 mm, width 1,22 mm, height 0,65 mm.

Metathoracic wings absent. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines complete.

Legs: Male hind femora broadened distally (fig. 96). Tarsal formula: ♂ 5-5-4, ♀ 5-4-4.

Male copulatory organ (figs 78-80): Aedeagus very slender, with proximal part simple and apex bent up, lateral margins gently converging toward subacute apex, ventral piece not bifid. Parameres slender, gently narrowing toward apex.

Spermatheca (fig. 114): Both basal and apical parts elongate, similar in length; the former larger.

HOLOTYPE ♂: Taichung Hsien, Hsuehshan, near Hsuehshan Tun-Feng, 3170 m, 11.V.1991, in MHNG.

PARATYPES: Together with the holotype, 11 ♂ and 10 ♀ in MHNG, 3 ♂ and 2 ♀ in NMNT, 4 ♂ and 3 ♀ in AC; same locality, 3170 m, 7.V.1991, 5 ♂ and 3 ♀ in MHNG, 3 ♂ and 2 ♀ in NMNT, 3 ♂ and 3 ♀ in AC; Anmashan, 2225 m, 2.V.1990, 1 ♂ in MHNG; Nantou Hsien, Houhuanshan, 3100 m, 20.IV.1990, 1 ♂ in MHNG; Meifeng, 2130 m, 13.V.1991, 2 ♂ and 2 ♀ in MHNG, 1 ♀ in AC; Hualien Hsien, Taroko N. P., Nanhushi Hut, 2220 m, 8.V.1990, 1 ♂ in MHNG; same locality, Chungyantienshi river, 2280 m, 10.V.1990, 1 ♂ and 1 ♀ in MHNG; same locality, ridge SE Nanhushi Hut, 2700 m, 11.V.1990, 1 ♂ and 3 ♀ in MHNG, 1 ♂ in AC; same locality, Nanhushi Hut, 2220 m, 12.V.1990, 1 ♂ in MHNG.

Discussion: See the discussion of *A. honestum*. *Agathidium lucidum* n.sp. is closely related to *A. tenebroides* n.sp., from which it differs by the more protuberant eyes and by the shape of the male copulatory organ.

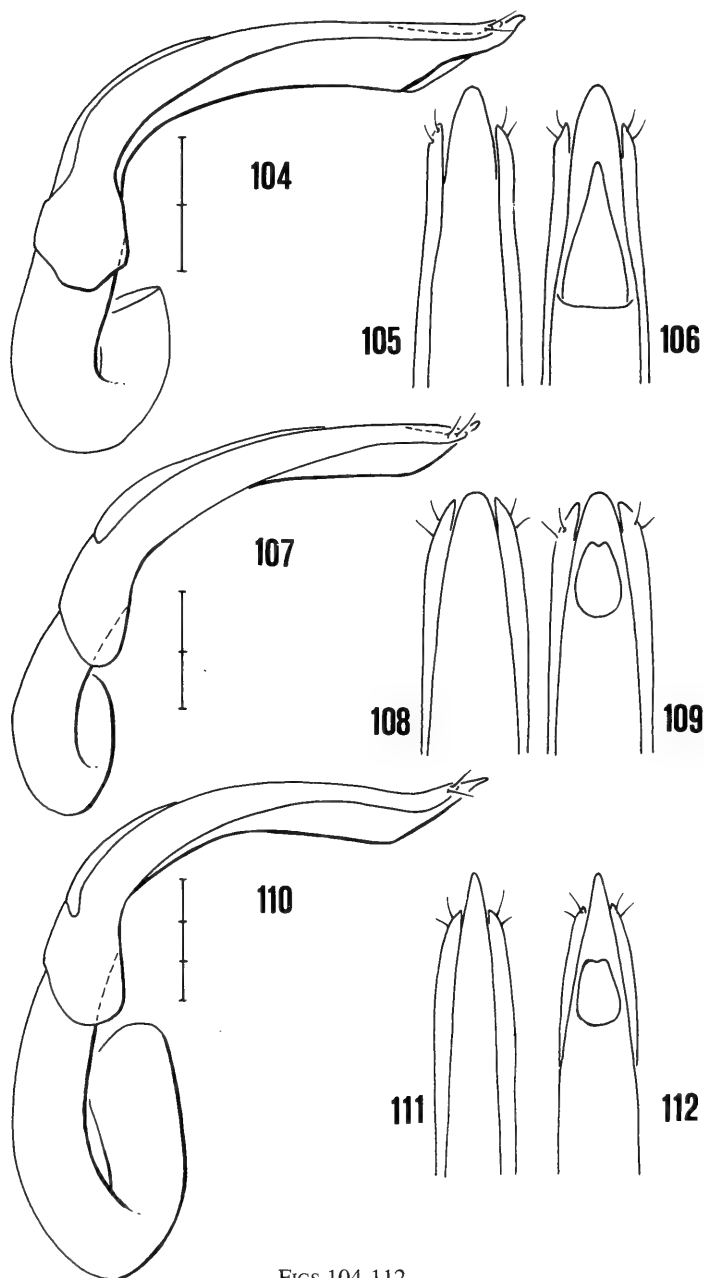
Habitats: Litter and various debris under broad-leaved trees along a river. Original broad-leaved forest, lush vegetation, debris and humus along a road. Original coniferous forest on northern slope. Open *Abies* forest. Original coniferous forest, rotting bark and wood, humus, moss and old mushrooms on and around fallen trees.

Distribution: Taiwan.

***Agathidium* (s.str.) *tenebroides* n.sp.**

Figs. 67, 97, 104-106, 115

Length 2,4-2,8 mm (holotype ♂ 2,70 mm). Entire dorsum reddish-brown; venter dark reddish-brown; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on entire dorsum, except for some traces on elytra; puncturation fine and sparse on head and pronotum, absent on elytra.



FIGS 104-112

Male copulatory organ (lateral view and dorsal/ventral view of its apex) of: 104-106, *Agathidium tenebroides* n.sp.; 107-109, *A. discretum* n.sp.; 110-112, *A. meifengense* n.sp.
Scales: 1 division = 0,1 mm.

Head: Widest at eyes (fig. 67); eyes flattened; clypeus slightly excavated; clypeal line absent; antero-lateral margins not raised. Third antennal segment as long as 2nd, shorter than 4th and 5th combined. Punctures small, superficial, spaced from each other by 2-10 times their own diameter.

Pronotum: 1,35 times as broad as head, slightly broader than long ($W/L = 1,35$), very convex ($W/H = 1,38$). Punctures as small as those on head, more superficial, spaced from each other by 4-10 times their own diameter. Holotype: length 0,90 mm, width 1,22 mm, height 0,88 mm.

Elytra: Slightly narrower than pronotum, as broad as long, moderately convex ($W/H = 1,79$); lateral outline with broadly rounded humeral angle; sutural striae absent. Only traces of microreticulation. Holotype: length 1,20 mm, width 1,15 mm, height 0,64 mm.

Metathoracic wings absent. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines incomplete.

Legs: Male hind femora simple (fig. 97). Tarsal formula: ♂ 5-5-4, ♀ 5-4-4.

Male copulatory organ (figs 104-106): Aedeagus very slender, with hook-like proximal part, lateral margins sinuate, apex rounded, ventral piece slender, not bifid. Parameres slender, gently narrowing toward apex.

Spermatheca (fig. 115): Both basal and apical parts elongate; the former longer and larger.

HOLOTYPE ♂: Chiai Hsien, Yushan N. P., Mun-Li Cliff, 1700 m, 27.IV.1990, in MHNG.

PARATYPES: Together with the holotype, 5 ♂ in MHNG, 3 ♂ and 1 ♀ in NMNT, 2 ♂ and 2 ♀ in AC; Nantou Hsien, Yushan N. P., Mun-Li Cliff, 2700 m, 18.V.1991, 5 ♂ and 3 ♀ in MHNG, 3 ♂ in NMNT, 2 ♂ and 1 ♀ in AC.

Discussion: See the discussion of *A. honestum* and *A. lucidum*.

Habitat: Original mixed coniferous and broad-leaved forest, plant debris and humus along bases of large rocks.

Distribution: Taiwan.

Agathidium (s.str.) discretum n.sp.

Figs. 82, 98, 107-109

Length 2,70 mm (holotype ♂). Entire dorsum dark reddish-brown; venter reddish-brown; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on entire dorsum, except for some traces on elytra; punctures very small on head and pronotum, nearly absent on elytra.

Head: Widest at eyes; eyes convex; clypeus sharply excavated; clypeal line absent; antero-lateral margins slightly raised. Third antennal segment 1,8 times as long as 2nd, shorter than 4th and 5th combined (fig. 82); Hamann's organ: gutter without vesicle in both 9th and 10th antennal segments. Punctures very small, superficial, spaced from each other by 4-10 times their own diameter.

Pronotum: 1,3 times as broad as head, moderately broader than long ($W/L = 1,41$), very convex ($W/H = 1,41$). Puncturation as that of head. Holotype: length 0,89 mm, width 1,26 mm, height 0,89 mm.

Elytra: Slightly broader than pronotum, slightly broader than long ($W/L = 1,13$), very little convex ($W/H = 2,09$); lateral outline with broadly rounded humeral

angle; sutural striae absent. Traces of microreticulation on entire surface; punctures sparse, very small. Holotype: length 1,15 mm, width 1,30 mm, height 0,62 mm.

Metathoracic wings absent. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines incomplete.

Legs: Male hind femora with large tooth (fig. 98). Tarsal formula: ♂ 5-5-4, ♀ not known.

Male copulatory organ (figs 107-109): Aedeagus very slender, with hook-like proximal part, lateral margins gently converging toward broadly rounded apex, ventral piece slightly emarginate. Parameres slender, gently narrowing toward apex.

HOLOTYPE ♂: Pingtung Hsien, Peitawushan, Kuai-Ku Hut, 2325 m, 21.V.1991, in MHNG.

Discussion: *Agathidium discretum* n.sp. shares most of the external features with the following 17 species of *laevigatum* group. Its distinctive character, in addition to shape of the male copulatory organ, is the ratio of 3rd/2nd antennal segments.

Habitat: Original broad-leaved forest, fallen leaves and other debris.

Distribution: Taiwan.

***Agathidium* (s.str.) *meifengense* n.sp.**

Figs. 83, 99, 110-112

Length 4,10 mm (holotype ♂ and paratypes). Entire dorsum black; venter dark reddish-brown, paler at mesosternum; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on entire dorsum, except for some traces on elytra; punctures very small on head and pronotum, larger on elytra.

Head: Widest at eyes; eyes convex; clypeus sharply excavated; clypeal line absent; antero-lateral margins not raised. Third antennal segment 1,5 times as long as 2nd, longer than 4th and 5th combined (fig. 83); Hamann's organ: gutter without vesicle in both 9th and 10th antennal segments. Punctures very small, superficial, spaced from each other by 4-20 times their own diameter.

Pronotum: 1,37 times as broad as head, vaguely broader than long (W/L = 1,17), very convex (W/H = 1,1,39). Punctures as small and sparse as those on head. Holotype: length 1,58 mm, width 1,85 mm, height 0,33 mm.

Elytra: Narrower than pronotum, as broad as long, moderately convex (W/H = 1,72); lateral outline with broadly rounded humeral angle; sutural striae absent. Only traces of microreticulation; punctures large, superficial, spaced from each other by 3-10 times their own diameter. Holotype: length 1,72 mm, width 1,78 mm, height 1,03 mm.

Metathoracic wings absent. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines incomplete.

Legs: Male hind femora with a large tooth (fig. 99). Tarsal formula: ♂ 5-5-4, ♀ not known.

Male copulatory organ (figs 110-112): Aedeagus very slender, with hook-like proximal part, lateral margins gently converging toward subacute apex, ventral piece deeply split. Parameres slender, gently narrowing toward apex.

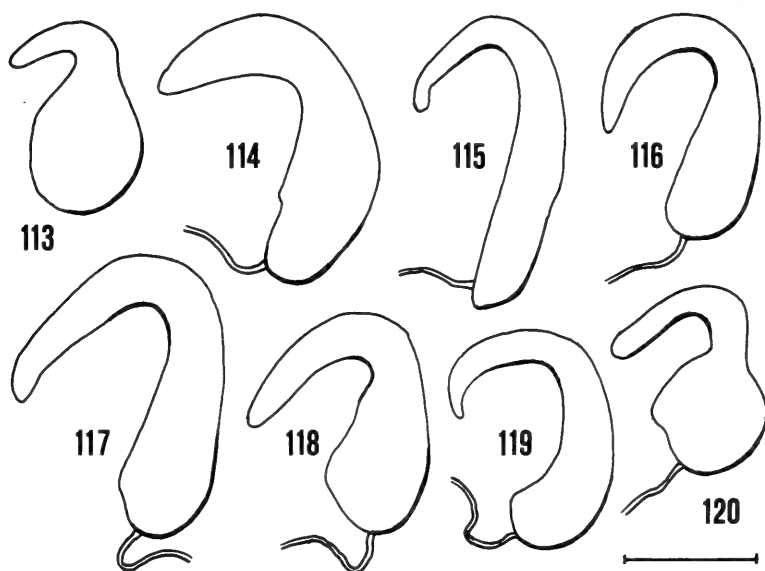
HOLOTYPE ♂: Nantou Hsien, Meifeng, 2130 m, 13.V.1991, in MHNG.

PARATYPES: Together with the holotype, 1 ♂ in NMNT, 1 ♂ in AC; Taichung Hsien, An-mashan, 2230 m, 4.V.1990, 1 ♂ in MHNG.

Discussion: *Agathidium meifengense* n.sp. shares most external features with the following species of *laevigatum* group. Its distinctive character, in addition to the shape of the male copulatory organ, is the size.

Habitat: Original broad-leaved forest, lush vegetation, debris and humus along a road.

Distribution: Taiwan.



FIGS 113-120

Spermatheca of: 113, *Agathidium glabricolle* n.sp.; 114, *A. lucidum* n.sp.; 115, *A. tenebroides* n.sp.; 116, *A. tessellatum* n.sp.; 117, *A. memnonium* n.sp.; 118, *A. kaohsiungense* n.sp.; 119, *A. angustatum* n.sp.; 120, *A. alpestre* n.sp. Scale: 1 division = 0,1 mm.

***Agathidium* (s.str.) *tessellatum* n.sp.**

Figs. 68, 69, 100, 116, 139-141

Length 2,9-3,2 mm (holotype ♂ 3,20 mm). Entire dorsum and venter reddish-brown; antennae uniformly testaceous; legs reddish-brown. Microreticulation vague on head and pronotum, superficial and uniform on elytra; puncturation fine on head and pronotum, absent on elytra.

Head: Punctures small, superficial, spaced from each other by 2-4 times their own diameter. Widest at eyes (fig. 68); eyes convex; clypeus moderately excavated; clypeal line absent; antero-lateral margins not raised. Third antennal segment 1,3 times as long as 2nd, shorter than 4th and 5th combined. Only traces of microreticulation.

Pronotum: 1,25 times as broad as head, slightly broader than long ($W/L = 1,36$), moderately convex ($W/H = 1,53$). Dorsal and lateral outlines: fig. 69. Only traces of microreticulation; punctures as small as those on head, spaced from each other by 2-5 times their own diameter. Holotype: length 1,10 mm, width 1,50 mm, height 0,98 mm.

Elytra: Slightly narrower than pronotum, as broad as long, moderately convex ($W/H = 1,68$); lateral outline with broadly rounded humeral angle; sutural striae absent. Traces of microreticulation on entire surface. Holotype: length 1,40 mm, width 1,40 mm, height 0,83 mm.

Metathoracic wings absent. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines complete.

Legs: Male hind femora simple (fig. 100). Tarsal formula: ♂ 5-5-4, ♀ 5-4-4.

Male copulatory organ (figs 139-141): Aedeagus very slender, with proximal part hook-like and apex bent up, lateral margins sinuate, apex broadly rounded, ventral piece very small. Parameres slender, gently narrowing toward apex.

Spermatheca (fig. 116): Basal part pyriform, apical part elongate.

HOLOTYPE ♂: Taichung Hsien, Hsuehshan, near Hsuehshan Tun-Feng, 3170 m, 7.V.1991, in MHNG.

PARATYPES: Together with the holotype, 1 ♀ in NMNT, 1 ♂ in AC.

Discussion: See the discussion of *A. discretum* and *A. meifengense*. *Agathidium tessellatum* n.sp. is remarkably similar in the external characters to the following species of *laevigatum* group. An interesting taxonomic character is the shape of the male hind femora, which are either simple or enlarged distally, or with a more or less pronounced tooth, which is curved in some instances. Based on that, *A. tessellatum* is close to *A. memnonium* n.sp., from which it differs by the size, by the ratio of 3rd/2nd antennal segments, by the ratio width/length of pronotum and by the less protuberant eyes.

Habitat: Original coniferous forest on northern slope, dead vegetation, rotting bark, wood and moss.

Distribution: Taiwan.

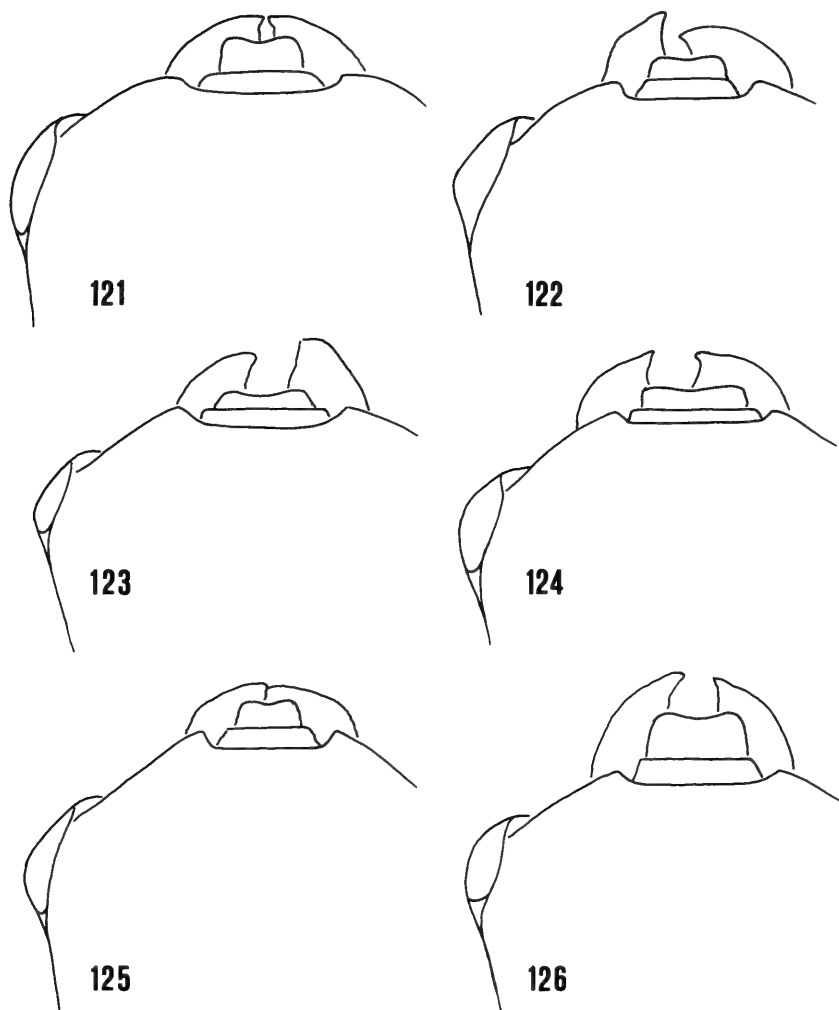
***Agathidium* (s.str.) *memnonium* n.sp.**

Figs. 70, 71, 101, 117, 142-144

Length 3,3-3,5 mm (holotype ♂ 3,45 mm). Entire dorsum reddish-brown; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on head and pronotum, superficial and uniform on elytra; punctures very small on head and pronotum, absent on elytra.

Head: Widest at eyes (fig. 70); eyes convex; clypeus moderately excavated; clypeal line absent; antero-lateral margins not raised. Third antennal segment 1,5 times as long as 2nd, longer than 4th and 5th combined. Punctures very small, superficial, spaced from each other by 1-10 times their own diameter.

Pronotum: 1,31 times as broad as head, slightly broader than long ($W/L = 1,27$), very convex ($W/H = 1,47$). Dorsal and lateral outlines: fig. 71. Punctures as small as those on head, sparser, spaced from each other by 5-10 times their own diameter. Holotype: length 1,22 mm, width 1,55 mm, height 1,05 mm.



FIGS 121-126

Head of: 121, *Agathidium kaohsiungense* n.sp.; 122, *A. chalconotum* n.sp.; 123, *A. angustatum* n.sp.; 124, *A. fuliginosum* n.sp.; 125, *A. subalpinum* n.sp.; 126, *A. intricatum* n.sp.

Elytra: Slightly narrower than pronotum, as broad as long, moderately convex ($W/H = 1,71$); lateral outline with broadly rounded humeral angle; sutural striae absent. Microreticulation superficial, uniform. Holotype: length 1,48 mm, width 1,46 mm, height 0,85 mm.

Metathoracic wings absent. Meso- and metasternum: median carina weak, lateral lines absent, femoral lines incomplete.

Legs: Male hind femora simple (fig. 101). Tarsal formula: ♂ 5-5-4, ♀ 5-4-4.

Male copulatory organ (figs 142-144): Aedeagus very slender, with proximal part hook-like and apex bent up, lateral margins sinuate, apex broadly rounded, ventral piece deeply bifid. Parameres slender, gently narrowing toward apex.

Spermatheca (fig. 117): Basal part pyriform, apical part elongate.

HOLOTYPE ♂: Hualien Hsien, Taroko N. P., ridge SE Nanhushi Hut, 2700 m, 11.V.1990, in MHNG.

PARATYPES: Together with the holotype, 1 ♀ in NMNT, 1 ♂ in AC.

Discussion: See the discussion of *A. tessellatum*.

Habitat: Original coniferous forest, rotting bark and wood, humus, moss and old mushrooms on and around fallen trees.

Distribution: Taiwan.

Agathidium (s.str.) kaohsiungense n.sp.

Figs. 84, 102, 118, 121, 145-147

Length 3.0-3.1 mm (holotype ♂ 3.0 mm). Entire dorsum black; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on head and pronotum, vague on elytra; punctures very small on head and pronotum, absent on elytra.

Head: Widest at eyes (fig. 121); eyes convex; clypeus moderately excavated; clypeal line absent; antero-lateral margins slightly raised. Third antennal segment 1.2 times as long as 2nd, as long as 4th and 5th combined (fig. 84); Hamann's organ: gutter without vesicle in both 9th and 10th antennal segments. Punctures very small, hardly visible.

Pronotum: 1.29 times as broad as head, moderately broader than long ($W/L = 1.4$), moderately convex ($W/H = 1.56$). Punctures as small as those on head, sparser, spaced from each other by 5-10 times their own diameter. Holotype: length 1.05 mm, width 1.47 mm, height 0.94 mm.

Elytra: Narrower than pronotum, slightly broader than long ($W/L = 1.06$), moderately convex ($W/H = 1.81$); lateral outline with broadly rounded humeral angle; sutural striae absent. Traces of microreticulation on entire surface. Holotype: length 1.30 mm, width 1.38 mm, height 0.76 mm.

Metathoracic wings absent. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines complete.

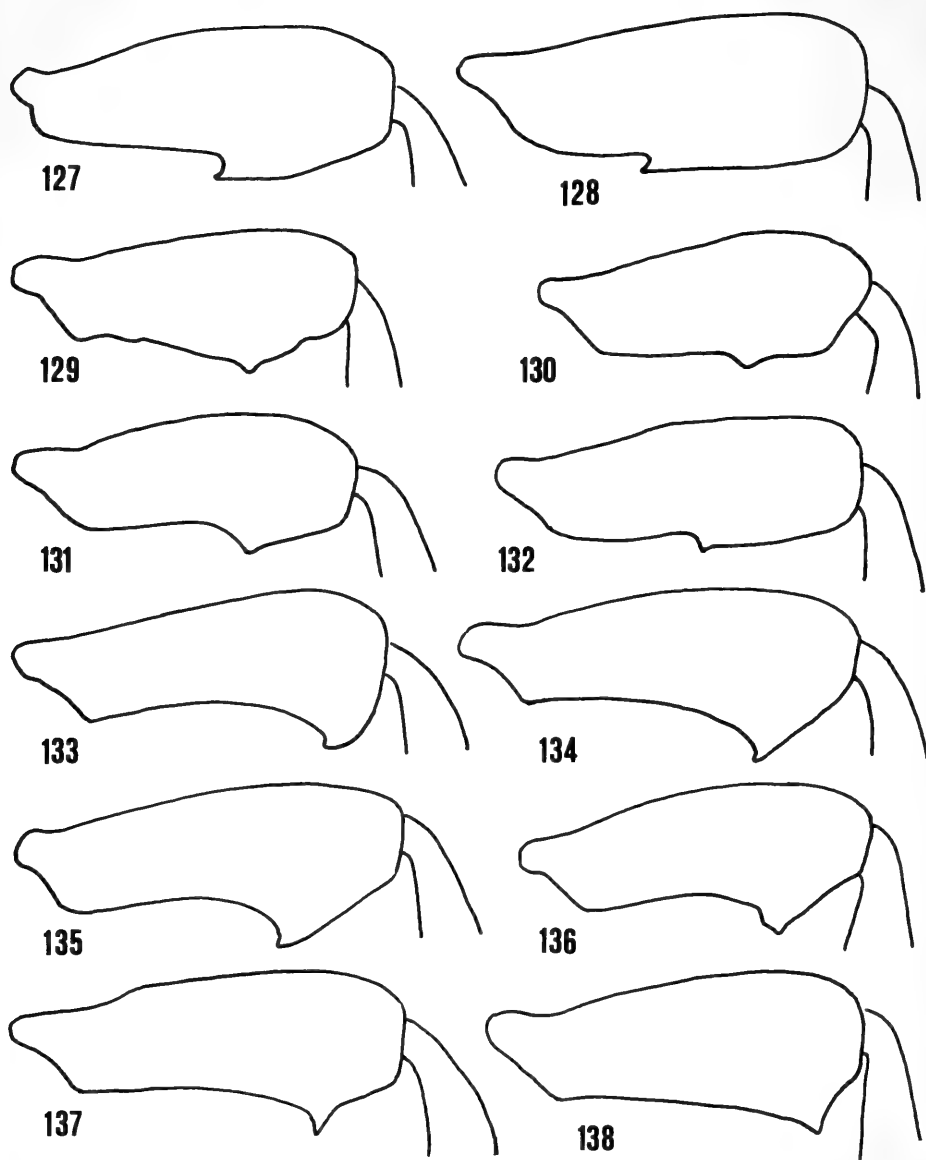
Legs: Male hind femora with small subdistal tooth (fig. 102). Tarsal formula: ♂ 5-5-4, ♀ 5-4-4.

Male copulatory organ (figs 145-147): Aedeagus slender, with proximal part ring-like and apex bent up, lateral margins gently converging toward rounded apex, ventral piece slightly emarginate. Parameres slender, gently narrowing toward apex.

Spermatheca (fig. 118): Basal part pyriform, apical part elongate.

HOLOTYPE ♂: Kaohsiung Hsien, Tengchih, 1535 m, 23.IV.1990, in MHNG.

PARATYPES: Together with the holotype, 3 ♀ in MHNG, 2 ♀ in NMNT, 2 ♀ in AC; same locality, 1610 m, 24.IV.1990, 1 ♀ in MHNG, 1 ♀ in AC; Pingtung Hsien, Peitawushan, Kuai-Ku Hut, 2325 m, 21.V.1991, 1 ♀ in MHNG.



Figs 127-138

Male hind femur of: 127, *Agathidium angustatum* n.sp.; 128, *A. fuliginosum* n.sp.; 129, *A. alpestre* n.sp.; 130, *A. furcatum* n.sp.; 131, *A. comptum* n.sp.; 132, *A. egregium* n.sp.; 133, *A. amashanense* n.sp.; 134, *A. subalpinum* n.sp.; 135, *A. intricatum* n.sp.; 136, *A. inustum* n.sp.; 137, *A. taichungense* n.sp.; 138, *A. exoletum* n.sp.

Discussion: *Agathidium kaohsiungense* n.sp. differs from *A. chalconotum* n.sp. by the colour of the dorsum, by the ratio of 3rd/2nd antennal segments and by the shape of the male hind femora, which are devoid of a true tooth in both species.

Habitats: Coniferous forest of *Taiwanis cryptomeroides*. Large clearing in a broad-leaved forest, dead vegetation and humus, rotting bark and wood along fallen trees and stumps.

Distribution: Taiwan.

Agathidium (s.str.) chalconotum n.sp.

Figs. 85, 103, 122, 148-150

Length 2,85 mm (holotype ♂). Entire dorsum reddish-brown; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on head and pronotum, vague on elytra; punctures very small on head and pronotum, nearly absent on elytra.

Head: Widest at eyes (fig. 122); eyes convex; clypeus slightly excavated; clypeal line absent; antero-lateral margins slightly raised. Third antennal segment 1,5 times as long as 2nd, as long as 4th and 5th combined (fig. 85); Hamann's organ: gutter without vesicle in both 9th and 10th antennal segments. Punctures very small, superficial, spaced from each other by 3-10 times their own diameter.

Pronotum: 1,5 times as broad as head, slightly broader than long ($W/L = 1,37$), very convex ($W/H = 1,31$). Punctures as small as those on head, spaced from each other by 3-20 times their own diameter. Holotype: length 0,95 mm, width 1,30 mm, height 0,99 mm.

Elytra: Narrower than pronotum, slightly broader than long ($W/L = 1,05$), slightly convex ($W/H = 2,06$); lateral outline with broadly rounded humeral angle; sutural striae absent. Traces of microreticulation on entire surface; sparse, very small punctures. Holotype: length 1,21 mm, width 1,28 mm, height 0,62 mm.

Metathoracic wings absent. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines incomplete.

Legs: Male hind femora with distal tooth (fig. 103). Tarsal formula: ♂ 5-5-4, ♀ not known.

Male copulatory organ (figs 148-150): Aedeagus very slender, with hook-like proximal part, lateral margins gently converging toward rounded apex, ventral piece slightly emarginate. Parameres stout, gently narrowing toward apex.

HOLOTYPE ♂: Pingtung Hsien, Peitawushan, above Kuai-Ku Hut, 2325 m, 22.V.1991, in MHNG.

Discussion: See the discussion of *A.kaohsiungense*.

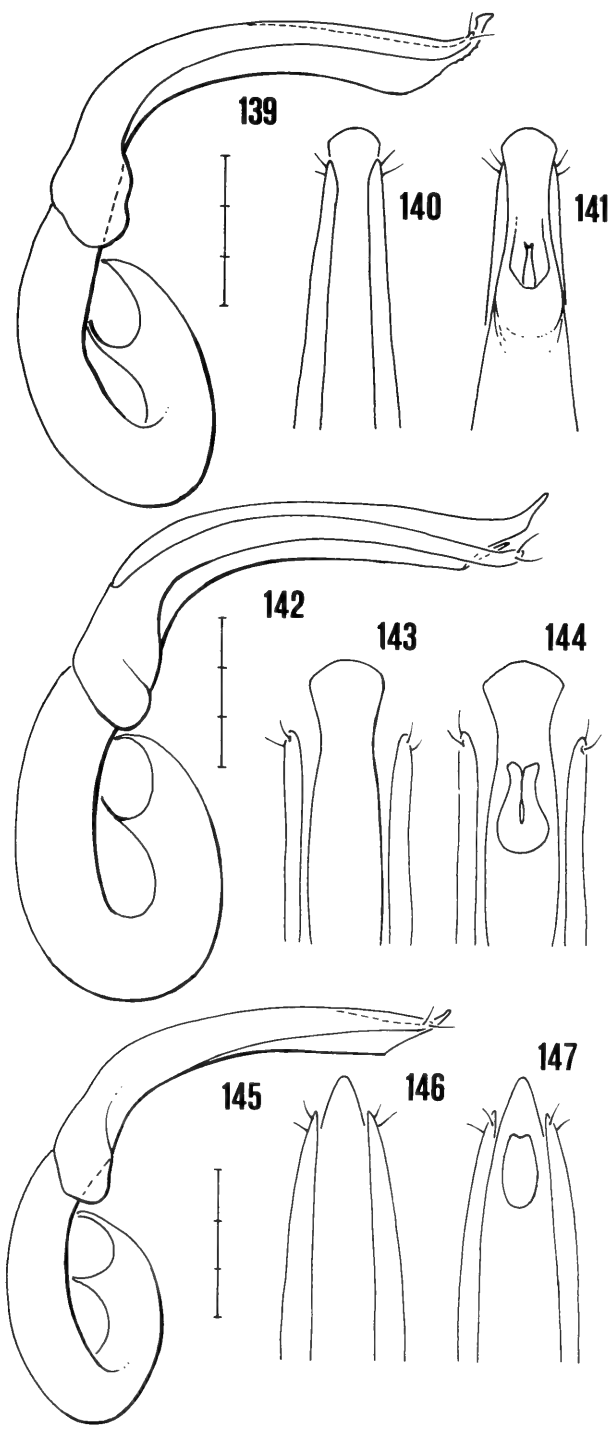
Habitat: Original broad-leaved forest, dead vegetation, fallen leaves and other debris.

Distribution: Taiwan.

Agathidium (s.str.) angustatum n.sp.

Figs. 86, 119, 123, 127, 151-153

Length 2,9-3,4 mm (holotype ♂ 3,40 mm). Entire dorsum dark reddish-brown; venter reddish-brown, paler at mesosternum; antennae uniformly testaceous; legs



reddish-brown. Microreticulation absent on head and pronotum, impressed on elytra; puncturation fine and sparse on head and pronotum, absent on elytra.

Head: Widest at eyes (123); eyes convex; clypeus slightly excavated; clypeal line absent; antero-lateral margins not raised. Third antennal segment 1,6 times as long as 2nd, shorter than 4th and 5th combined (fig. 86). Punctures small, superficial, spaced from each other by 2-4 times their own diameter.

Pronotum: 1,31 times as broad as head, slightly broader than long ($W/L = 1,37$), moderately convex ($W/H = 1,54$). Puncturation as that of head. Holotype: length 1,12 mm, width 1,54 mm, height 1,00 mm.

Elytra: Slightly narrower than pronotum, as broad as long, moderately convex ($W/H = 1,85$); lateral outline with broadly rounded humeral angle; sutural striae absent. Microreticulation impressed, uniform, superficial in one paratype. Holotype: length 1,50 mm, width 1,50 mm, height 0,81 mm.

Metathoracic wings absent. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines complete.

Legs: Male hind femora with a very sharp, curved tooth (fig. 127). Tarsal formula: ♂ 5-5-4, ♀ 5-4-4.

Male copulatory organ (figs 151-153): Aedeagus very slender, with proximal part hook-like and apex bent up, lateral margins sinuate, apex enlarged and broadly rounded, ventral piece slightly emarginate. Parameres slender, gently narrowing toward apex.

Spermatheca (fig. 119): Both basal and apical parts elongate; the former larger.

HOLOTYPE ♂: Taichung Hsien, Hsuehshan, near Hsuehshan Tun-Feng, 3170 m, 7.V.1991, in MHNG.

PARATYPES: Together with the holotype, 1 ♀ in NMNT, 1 ♂ in AC; same locality, 3170 m, 11.V.1991, 1 ♂ in MHNG, 1 ♀ in AC.

Discussion: *Agathidium angustatum* n.sp. shares the shape of the male hind femora, bearing a hook-like tooth, with *A. fuliginosum* n.sp. It differs from it by the size, the colour of the dorsum and by the shape of the head.

Habitat: Original coniferous forest on northern slope dead vegetation, rotting bark, wood and moss.

Distribution: Taiwan.

***Agathidium* (s.str.) *fuliginosum* n.sp.**

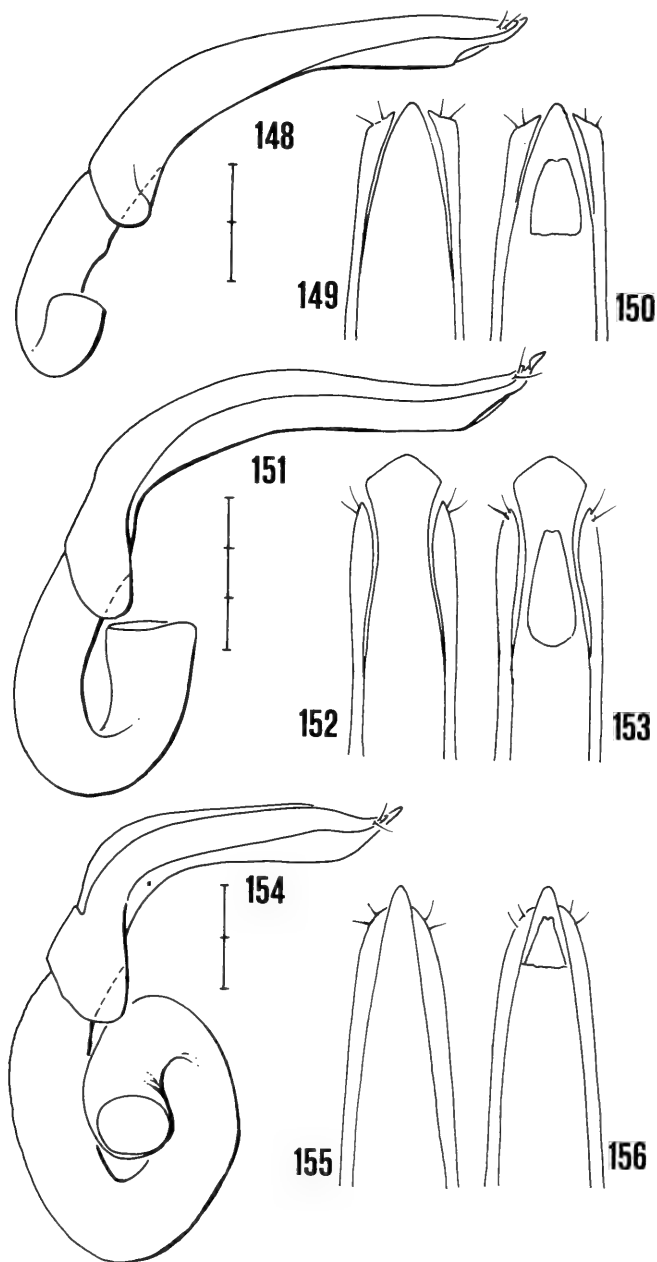
Figs. 87, 124, 128, 154-156

Length 3,5 mm (holotype ♂). Entire dorsum black; venter dark reddish-brown, paler at mesosternum; antennae uniformly reddish-brown; legs reddish-brown. Micro-

FIGS 139-147

Male copulatory organ (lateral view and dorsal/ventral view of its apex) of: 139-141, *Agathidium tessellatum* n.sp.; 142-144, *A. memnonium* n.sp.; 145-147, *A. kaohsiungense* n.sp.

Scales: 1 division = 0,1 mm.



FIGS 148-156

Male copulatory organ (lateral view and dorsal/ventral view of its apex) of: 148-150, *Agathidium chalconotum* n.sp.; 151-153, *A. angustatum* n.sp.; 154-156, *A. fuliginosum* n.sp.
Scales: 1 division = 0,1 mm.

reticulation absent on head and pronotum, vague on elytra; punctures very small on head and pronotum, absent on elytra.

Head: Widest at eyes (fig. 124); eyes convex; clypeus moderately excavated; clypeal line absent; antero-lateral margins slightly raised. Third antennal segment 1,7 times as long as 2nd, as long as 4th and 5th combined (fig. 87); Hamann's organ: gutter without vesicle in both 9th and 10th antennal segments. Punctures small, superficial, spaced from each other by 6-15 times their own diameter.

Pronotum: 1,34 times as broad as head, slightly broader than long ($W/L = 1,3$), very convex ($W/H = 1,43$). Punctures as small and sparse as those on head. Holotype: length 1,23 mm, width 1,60 mm, height 1,12 mm.

Elytra: Narrower than pronotum, as broad as long, moderately convex ($W/H = 1,73$); lateral outline with broadly rounded humeral angle; sutural striae absent. Traces of microreticulation on entire surface. Holotype: length 1,50 mm, width 1,53 mm, height 0,88 mm.

Metathoracic wings absent. Meso- and metasternum: median carina weak, lateral lines absent, femoral lines complete.

Legs: Male hind femora with a sharp, curved tooth (fig. 128). Tarsal formula: ♂ 5-5-4, ♀ not known.

Male copulatory organ (figs 154-156): Aedeagus very slender, with spiralled proximal part, lateral margins gently converging toward rounded apex, ventral piece slightly emarginate. Parameres stout, gently narrowing toward apex.

Holotype ♂: Pingtung Hsien, Peitawushan, Kuai-Ku Hut, 2325 m, 21.V.1991, in MHNG.

Discussion: See the discussion of *A. angustatum*.

Habitat: Original broad-leaved forest, fallen leaves and other debris.

Distribution: Taiwan.

Agathidium (s.str.) alpestre n.sp.

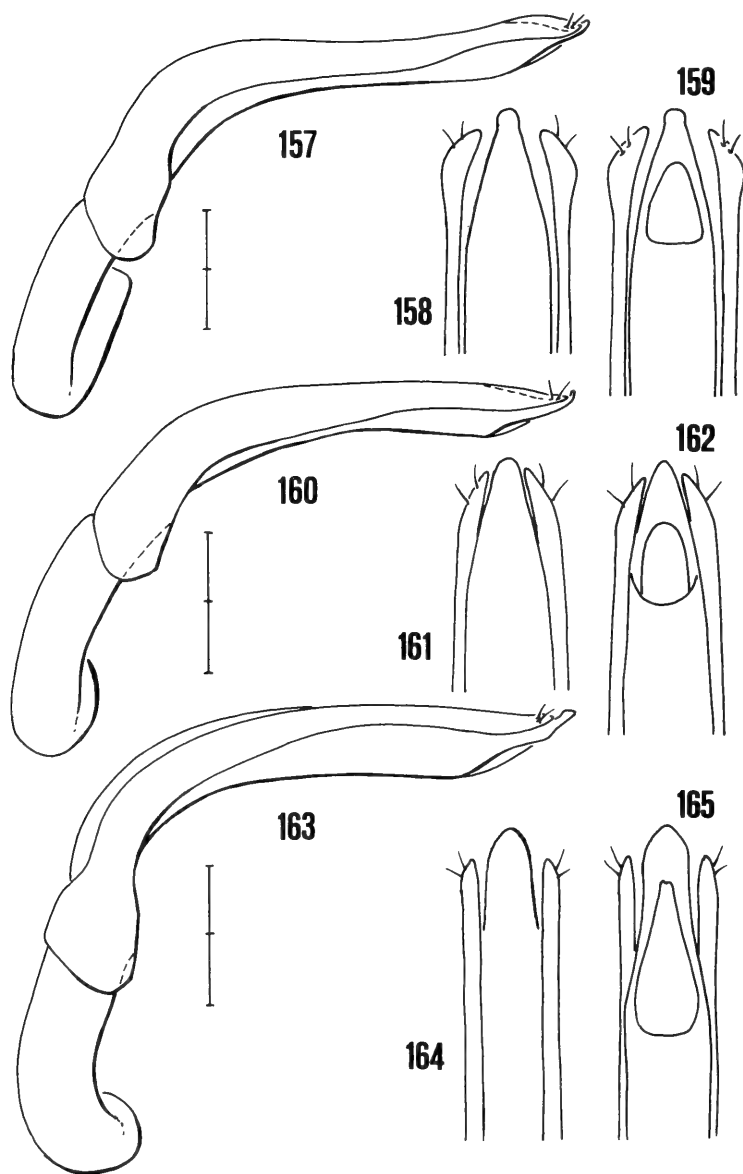
Figs. 88, 120, 129, 157-159

Length 3,0-3,2 mm (holotype ♂ 3,15 mm). Entire dorsum black; venter reddish-brown; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on head and pronotum, superficial on elytra; puncturation fine and sparse on entire dorsum.

Head: Widest at eyes; eyes convex; clypeus moderately excavated; clypeal line absent; antero-lateral margins not raised. Third antennal segment 1,2 times as long as 2nd, as long as 4th and 5th combined (fig. 88); Hamann's organ: gutter without vesicle in both 9th and 10th antennal segments. Punctures small, superficial, spaced from each other by 10 times their own diameter.

Pronotum: 1,33 times as broad as head, slightly broader than long ($W/L = 1,23$), very convex ($W/H = 1,43$). Puncturation as that of head. Holotype: length 1,10 mm, width 1,36 mm, height 0,95 mm.

Elytra: Slightly narrower than pronotum, as broad as long, moderately convex ($W/H = 1,83$); lateral outline with broadly rounded humeral angle; sutural striae absent. Microreticulation very superficial or vague; puncturation as that of head. Holotype: length 1,35 mm, width 1,32 mm, height 0,72 mm.



FIGS 157-165

Male copulatory organ (lateral view and dorsal/ventral view of its apex) of: 157-159, *Agathidium alpestre* n.sp.; 160-162, *A. furcatum* n.sp.; 163-165, *A. comptum* n.sp. Scales: 1 division = 0,1 mm.

Metathoracic wings absent. Meso- and metasternum: median carina weak, lateral lines absent, femoral lines complete.

Legs: Male hind femora with small subdistal tooth (fig. 129). Tarsal formula: ♂ 5-5-4, ♀ 5-4-4.

Male copulatory organ (figs 157-159): Aedeagus very slender, with hook-like proximal part, lateral margins gently converging toward rounded apex, ventral piece not bifid. Parameres stout, gently narrowing toward apex.

Spermatheca (fig. 120): Basal part globose, apical part elongate.

HOLOTYPE ♂: Nantou Hsien, Yushan N. P., Pai-Yun Hut, 2 Km W Pai-Yun Hut, 3350 m, 16.V.1991, in MHNG.

PARATYPES: Together with the holotype, 1 ♂ and 1 ♀ in AC; Meifeng, 2130 m, 13.V.1991, 1 ♂ and 2 ♀ in MHNG, 1 ♀ in NMNT.

Discussion: *Agathidium alpestre* n.sp. shares with *A. furcatum* n.sp., *A. compactum* n.sp. and *A. egregium* n.sp., the presence of a comparatively small subdistal tooth on the male hind femora; in addition to the shape of the male copulatory organ, the distinctive features of *A. alpestre* are the size and the colour of dorsum.

Habitats: Original broad-leaved forest, lush vegetation, debris and humus along a road. Original *Abies* forest, rotting bark and wood along fallen trees.

Distribution: Taiwan.

***Agathidium* (s.str.) *furcatum* n.sp.**

Figs. 89, 130, 160-162

Length 2,60 mm (holotype ♂). Entire dorsum reddish-brown; venter reddish-brown, paler at mesosternum; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on head and pronotum, superficial on elytra; punctures very small on head and pronotum, absent on elytra.

Head: Widest at eyes; eyes convex; clypeus sharply excavated; clypeal line absent; antero-lateral margins not raised. Third antennal segment 1,1 times as long as 2nd, as long as 4th and 5th combined (fig. 89); Hamann's organ: gutter without vesicle in both 9th and 10th antennal segments. Only some very small punctures.

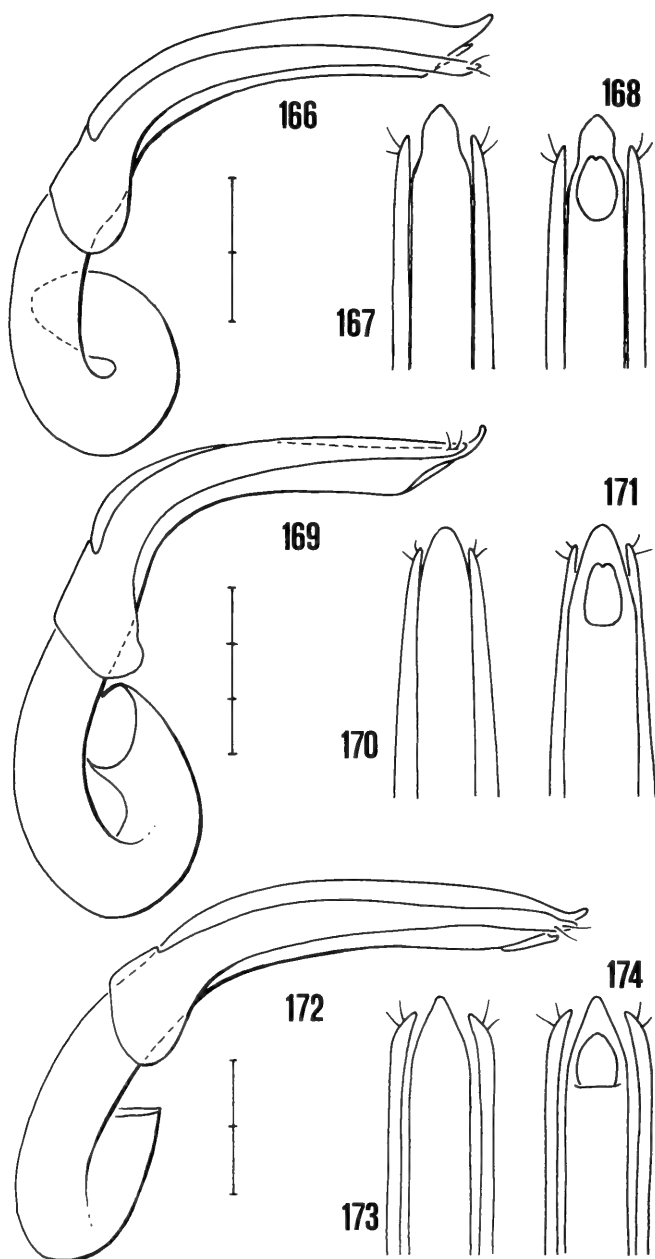
Pronotum: 1,23 times as broad as head, slightly broader than long (W/L = 1,23), very convex (W/H = 1,37). Punctures as small as those on head, spaced from each other by 1-6 times their own diameter. Holotype: length 0,87 mm, width 1,07 mm, height 0,78 mm.

Elytra: As broad as pronotum, as broad as long, moderately convex (W/H = 1,84); lateral outline with broadly rounded humeral angle; sutural striae absent. Microreticulation superficial. Holotype: length 1,10 mm, width 1,07 mm, height 0,58 mm.

Metathoracic wings absent. Meso- and metasternum: median carina weak, lateral lines absent, femoral lines incomplete.

Legs: Male hind femora with small subdistal tooth (fig. 130). Tarsal formula: ♂ 5-5-4, ♀ not known.

Male copulatory organ (figs 160-162): Aedeagus very slender, with hook-like proximal part, lateral margins gently converging toward rounded apex, ventral piece not bifid. Parameres stout, gently narrowing toward apex.



FIGS 166-174

Male copulatory organ (lateral view and dorsal/ventral view of its apex) of: 166-168, *Agathidium egregium* n.sp.; 169-171, *A. ammashanense* n.sp.; 172-174, *A. subalpinum* n.sp.
 Scales: 1 division = 0,1 mm.

Holotype ♂: Kaohsiung Hsien, Tengchih, 1535 m, 23.IV.1990, in MHNG.

Discussion: See the discussion of *A. alpestre*. *Agathidium furcatum* n.sp. differs from *A. comptum* n.sp. and *A. egregium* n.sp. by the ratio of 3rd/2nd antennal segments and by the shape of the parameres.

Habitat: Coniferous forest of *Taiwania cryptomeroides*, fallen twigs, humus and other debris, mainly along fallen trees.

Distribution: Taiwan.

***Agathidium* (s.str.) *comptum* n.sp.**

Figs. 90, 131, 163-165, 181

Length 2,6-2,7 mm (holotype ♂ 2,65 mm). Entire dorsum dark reddish-brown or black; venter reddish-brown; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on head and pronotum, superficial or vague on elytra; punctures very small on entire dorsum.

Head: Widest at eyes; eyes convex; clypeus slightly excavated; clypeal line absent; antero-lateral margins not raised. Third antennal segment 1,2 times as long as 2nd, shorter than 4th and 5th combined (fig. 90); Hamann's organ: gutter without vesicle in both 9th and 10th antennal segments. Only traces of microreticulation. Punctures very small, superficial, spaced from each other by 3-10 times their own diameter.

Pronotum: 1,35 times as broad as head, slightly broader than long ($W/L = 1,3$), very convex ($W/H = 1,3$). Punctures as small as those on head. Holotype: length 0,88 mm, width 1,15 mm, height 0,88 mm.

Elytra: As broad as pronotum, as broad as long, moderately convex ($W/H = 1,61$); lateral outline with broadly rounded humeral angle; sutural striae absent. Microreticulation very superficial or vague on entire surface; punctures as small as those on head. Holotype: length 1,15 mm, width 1,10 mm, height 0,68 mm.

Metathoracic wings absent. Meso- and metasternum: median carina weak, lateral lines complete, femoral lines complete.

Legs: Male hind femora with sharp sudistal tooth (fig. 131). Tarsal formula: ♂ 5-5-4, ♀ 5-4-4.

Male copulatory organ (figs 163-165): Aedeagus very slender, with hook-like proximal part, lateral margins sinuate, gently converging toward rounded apex, ventral piece very slender, slightly emarginate. Parameres slender, gently narrowing toward apex.

Spermatheca (fig. 181): Both basal and apical parts elongate; the former larger.

HOLOTYPE ♂: Nantou Hsien, Yushan N. P., Mun-Li Cliff, 2700 m, 13.V.1991, in MHNG.

PARATYPES: Together with the holotype, 1 ♀ in MHNG, 1 ♀ in NMNT; Kaohsiung Hsien, Tengchih, 1700-1800 m, 24.IV.1990, 1 ♂ and 1 ♀ in AC.

Discussion: See the discussion of *A. alpestre* and *A. furcatum*. *Agathidium egregium* n.sp. differs from *A. comptum* n.sp. by the presence of the traces of microreticulation on both the head and pronotum, and by the very small punctures on the elytra.

Habitat: Original broad-leaved forest, litter and plant debris.

Distribution: Taiwan.

Agathidium (s.str.) egregium n.sp.

Figs. 132, 166-168

Length 2,50 mm (holotype ♂). Entire dorsum dark reddish-brown; venter reddish-brown; antennae uniformly testaceous; legs reddish-brown. Microreticulation vague on head, superficial on elytra; punctures very small only on pronotum.

Head: Widest at eyes; eyes convex; clypeus slightly excavated; clypeal line absent; antero-lateral margins slightly raised. Third antennal segment 1,2 times as long as 2nd, longer than 4th and 5th combined. Only traces of microreticulation.

Pronotum: 1,33 times as broad as head, moderately broader than long ($W/L = 1,43$), moderately convex ($W/H = 1,53$). Punctures very small, superficial, spaced from each other by 2-10 times their own diameter. Holotype: length 0,80 mm, width 1,15 mm, height 0,75 mm.

Elytra: As broad as pronotum, as broad as long, slightly convex ($W/H = 1,88$); lateral outline with broadly rounded humeral angle; sutural striae absent. Microreticulation very superficial. Holotype: length 1,10 mm, width 1,15 mm, height 0,61 mm.

Metathoracic wings absent. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines complete.

Legs: Male hind femora with small subdistal tooth (fig. 132). Tarsal formula: ♂ 5-5-4, ♀ not known.

Male copulatory organ (figs 166-168): Aedeagus slender, with ring-like proximal part, lateral margins sinuate, abruptly converging toward rounded apex, ventral piece slightly emarginate. Parameres slender, gently narrowing toward apex.

HOLOTYPE ♂: Hualien Hsien, Taroko N. P., Nanhushi Hut, 2220 m, 12.V.1990, in MHNG.

Discussion: See the discussion of *A. alpestre*, *A. furcatum* and *A. comptum*.

Habitat: Original coniferous forest, rotting bark, wood and various debris near bases of large trees.

Distribution: Taiwan.

Agathidium (s.str.) anmashanense n.sp.

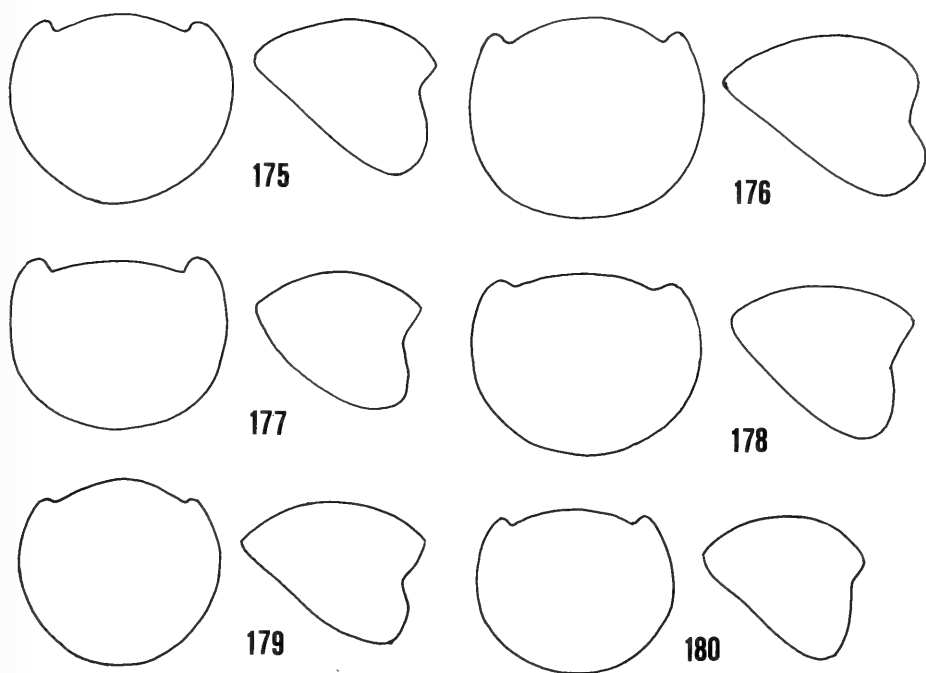
Figs. 133, 169-171, 182

Length 3,1-3,4 mm (holotype ♂ 3,40 mm). Entire dorsum black; venter reddish-brown; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on head and pronotum, vague on elytra; punctures very small on entire dorsum.

Head: Widest at eyes; eyes very convex; clypeus moderately excavated; clypeal line absent; antero-lateral margins slightly raised. Third antennal segment 1,2 times as long as 2nd, as long as 4th and 5th combined; Hamann's organ: gutter without vesicle in both 9th and 10th antennal segments. Punctures very small, hardly visible.

Pronotum: 1,28 times as broad as head, slightly broader than long ($W/L = 1,31$), moderately convex ($W/H = 1,55$). Punctures as small as those on head, superficial, spaced from each other by 5-15 times their own diameter. Holotype: length 1,22 mm, width 1,60 mm, height 1,07 mm.

Elytra: As broad as pronotum, slightly broader than long ($W/L = 1,08$), slightly convex ($W/H = 2,07$); lateral outline with broadly rounded humeral angle; sutural



FIGS 175-180

Pronotum (dorsal and lateral outline) of: 175, *Agathidium subalpinum* n.sp.; 176, *A. intricatum* n.sp.; 177, *A. taichungense* n.sp.; 178, *A. exoletum* n.sp.; 179, *A. fuscum* n.sp.; 180, *A. lunatum* n.sp.

striae absent. Traces of microreticulation on entire surface; punctures as small as those on head, spaced from each other by 2-20 times their own diameter. Holotype: length 1,47 mm, width 1,60 mm, height 0,77 mm.

Metathoracic wings absent. Meso- and metasternum: median carina absent, lateral lines absent, femoral lines complete.

Legs: Male hind femora with a sharp distal tooth (fig. 133). Tarsal formula: ♂ 5-5-4, ♀ 5-4-4.

Male copulatory organ (figs 169-171): Aedeagus slender, with ring-like proximal part, lateral margins parallel and then abruptly converging toward rounded apex, ventral piece slightly emarginate. Parameres slender, gently narrowing toward apex.

Spermatheca (fig. 182): Basal part pyriform, apical part elongate.

HOLOTYPE ♂: Taichung Hsien, Anmashan, 2225 m, 2.V.1990, in MHNG.

PARATYPES: Together with the holotype, 1 ♀ in NMNT; same locality, 2225 m, 3.V.1990, 1 ♂ and 1 ♀ in AC; Hsuehshan, near Hsuehshan Tun-Feng, 3170 m, 11.V.1991, 4 ♂ and 1 ♀ in MHNG; Hualien Hsien, Taroko N. P., Nanhushi Hut, 2220 m, 8.V.1990, 1 ♂ in MHNG.

Discussion: See the discussion of *A. tessellatum*. *Agathidium anmashanense* n.sp. shares with the following five species (*A. subalpinum* n.sp., *A. intricatum* n.sp., *A. inustum* n.sp., *A. taichungense* n.sp. and *A. exoletum* n.sp.) the possession of the large tooth on male hind femora; in addition too the shape of male copulatory organ, the distinctive feature of *A. anmashanense* is the absence of the mesosternal carina.

Habitats: Original broad-leaved forest, bark, wood, litter and various plant debris around bases of huge trees and along fallen trees. Original coniferous forest on northern slope, moss, dead vegetation and various debris. Original coniferous forest, rotting bark, wood and various debris near bases of large trees.

Distribution: Taiwan.

Agathidium (s.str.) subalpinum n.sp.

Figs. 125, 134, 172-175, 183

Length 3,0-3,3 mm (holotype ♂ 3,25 mm). Entire dorsum dark reddish-brown or black; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on head and pronotum, vague or superficial on elytra; puncturation fine and sparse on head and pronotum, absent on elytra.

Head: Widest at eyes (fig. 125); eyes convex; clypeus sharply excavated; clypeal line absent; antero-lateral margins not raised. Third antennal segment 1,2 times as long as 2nd, longer than 4th and 5th combined. Punctures very small, hardly visible.

Pronotum: 1,31 times as broad as head, slightly broader than long ($W/L = 1,18$), very convex ($W/H = 1,42$). Dorsal and lateral outlines: fig. 175. Punctures as small as those on head. Holotype: length 1,25 mm, width 1,48 mm, height 1,04 mm.

Elytra: Slightly narrower than pronotum, as broad as long, moderately convex ($W/H = 1,82$); lateral outline with broadly rounded humeral angle; sutural striae absent. Microreticulation very superficial or vague on entire surface; puncturation absent, except for some very small punctures. Holotype: length 1,35 mm, width 1,42 mm, height 0,78 mm.

Metathoracic wings absent. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines incomplete.

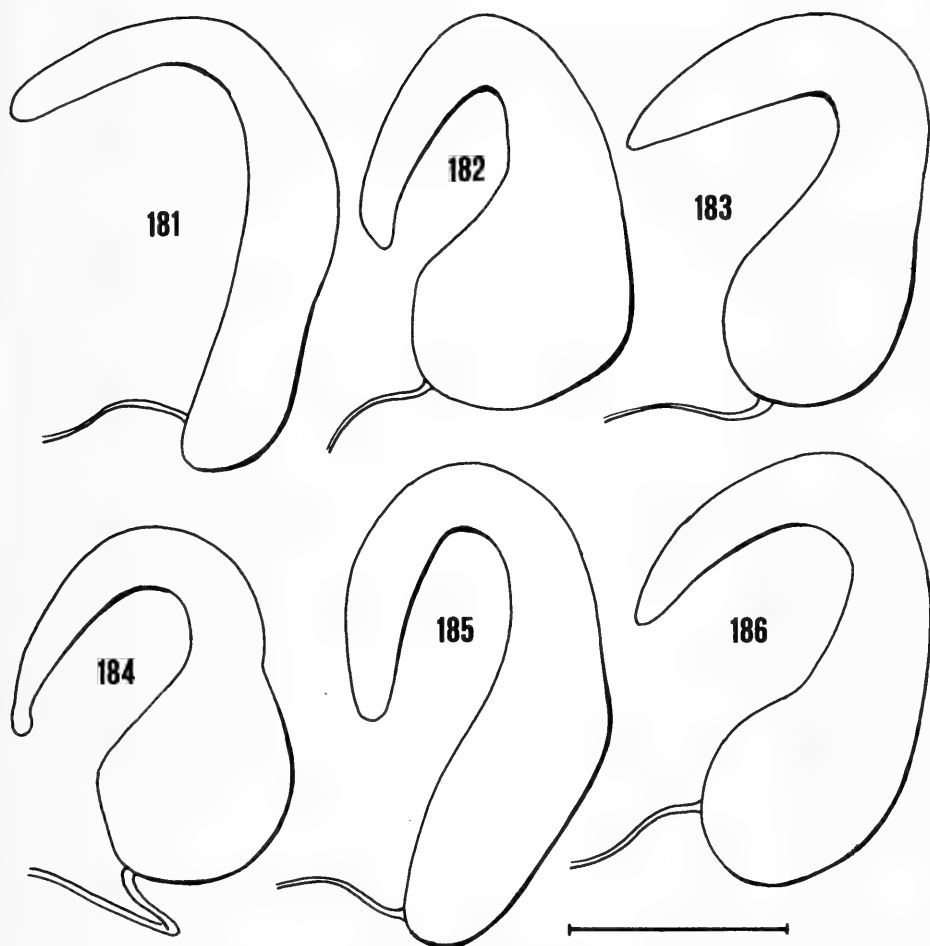
Legs: Male hind femora with a sharp distal tooth (fig. 134). Tarsal formula: ♂ 5-5-4, ♀ 5-4-4.

Male copulatory organ (figs 172-174): Aedeagus very slender, with hook-like proximal part, lateral margins parallel and then abruptly converging toward rounded apex, ventral piece not bifid. Parameres stout, gently narrowing toward apex.

Spermatheca (fig. 183): Basal part pyriform, apical part elongate.

HOLOTYPE ♂: Nantou Hsien, Houhuanshan, 3100 m, 20.IV.1990, in MHNG.

PARATYPES: Taichung Hsien, Hsuehshan, above Shan-Liu Gieu Hut, 3220 m, 7.V.1991, 1 ♂ in AC; same locality, near Hsuehshan Tun-Feng, 3170 m, 11.V.1991, 1 ♂ in MHNG, 1 ♀ in AC; Chi'ai Hsien, Yushan N. P., Mun-Li Cliff, 1700 m, 27.IV.1990, 1 ♂ in NMNT.

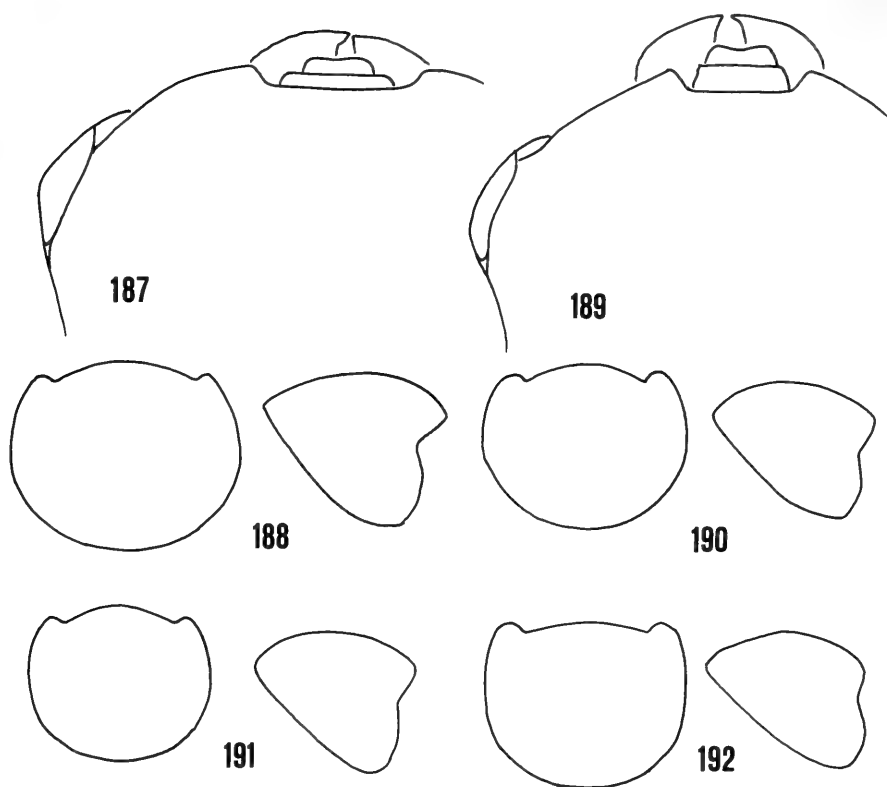


FIGS 181-186

Spermatheca of: 181, *Agathidium comptum* n.sp.; 182, *A. anmashanense* n.sp.; 183, *A. subalpinum* n.sp.; 184, *A. inustum* n.sp.; 185, *A. taichungense* n.sp.; 186, *A. exoletum* n.sp. Scale: 1 division = 0,1 mm.

Discussion: See the discussion of *A. anmashanense*. *Agathidium subalpinum* n.sp. differs from *A. intricatum* n.sp. by the size, the shape of the head, by the more enlarged male tarsi and by the absence of punctures on the elytra. The male copulatory organ is distinctive. *Agathidium subalpinum* shares with *A. intricatum* the shape of the pronotum and differs in this feature from *A. inustum* n.sp., *A. taichungense* n.sp. and *A. exoletum* n.sp.

Habitats: Original *Abies* forest, grasses and other vegetation, humus and various debris. Original coniferous forest on northern slope. Original mixed coniferous and broad-leaved forest, moss, litter and rotting bark and wood around huge trees.



FIGS 187-192

Head and/or pronotum (dorsal and lateral view) of: 187-188, *Agathidium umbratum* n.sp.; 189-190, *A. fenestratum* n.sp.; 191, *A. splendidulum* n.sp.; 192, *A. melanocephalum* n.sp.

Distribution: Taiwan.

***Agathidium* (s.str.) *intricatum* n.sp.**

Figs. 91, 126, 135, 176, 201-203

Length 3,55 mm (holotype ♂). Entire dorsum black; venter reddish-brown, paler at mesosternum; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on head and pronotum, vague on elytra; puncturation fine and sparse on entire dorsum.

Head: Widest at eyes (fig. 126); eyes convex; clypeus moderately excavated; clypeal line absent; antero-lateral margins not raised. Third antennal segment 1,2 times as long as 2nd, as long as 4th and 5th combined (fig. 91); Hamann's organ:

gutter without vesicle in both 9th and 10th antennal segments. Punctures very small, superficial, spaced from each other by 4-10 times their own diameter.

Pronotum: 1,29 times as broad as head, slightly broader than long ($W/L = 1,21$), very convex ($W/H = 1,43$). Dorsal and lateral outlines: fig. 176. Punctures as small and sparse as those on head. Holotype: length 1,30 mm, width 1,58 mm, height 1,10 mm.

Elytra: As broad as pronotum, as broad as long, slightly convex ($W/H = 1,88$); lateral outline with broadly rounded humeral angle; sutural striae absent. Traces of microreticulation on entire surface; punctures as small as those on head, spaced from each other by 1-10 times their own diameter. Holotype: length 1,50 mm, width 1,53 mm, height 0,81 mm.

Metathoracic wings absent. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines complete.

Legs: Male hind femora with a sharp, curved tooth (fig. 135). Tarsal formula: ♂ 5-5-4, ♀ not known.

Male copulatory organ (figs 201-203): Aedeagus very slender, with hook-like proximal part, lateral margins parallel and then abruptly converging toward enlarged apex, ventral piece not bifid. Parameres stout, gently narrowing toward apex.

HOLOTYPE ♂: Taichung Hsien, Hsuehshan, near Hsuehshan Tun-Feng, 3170 m, 11.V.1991, in MHNG.

PARATYPE: same locality, 3170 m, 7.V.1991, 1♂ in AC.

Discussion: See the discussion of *A. anmashanense* and *A. subalpinum*.

Habitat: Original coniferous forest on northern slope, dead vegetation, rotting bark, wood and moss.

Distribution: Taiwan.

***Agathidium* (s.str.) *inustum* n.sp.**

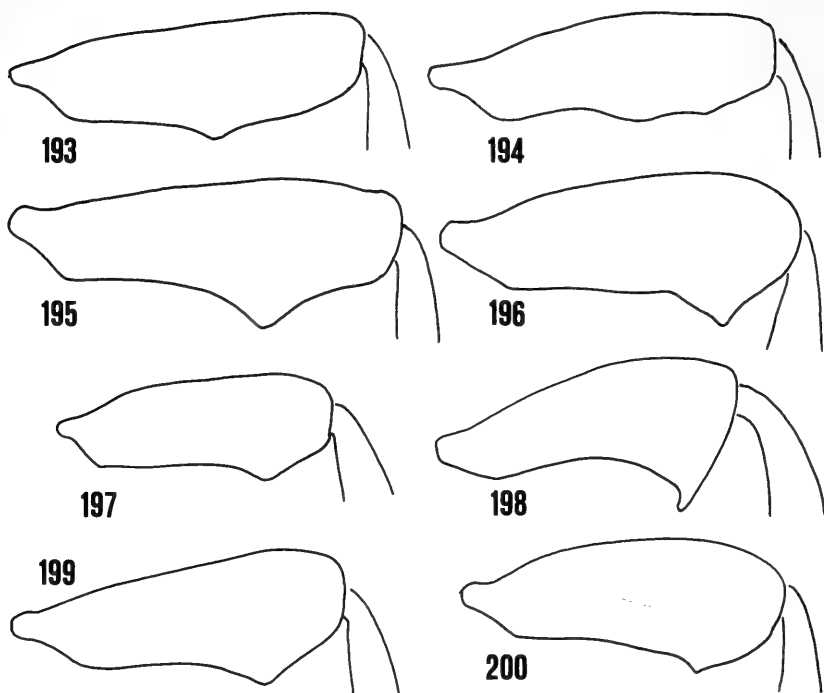
Figs. 136, 184, 204-206

Length 2,7-3,0 mm (holotype ♂ 3,00 mm). Entire dorsum black, reddish-brown along the suture; venter reddish-brown; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on head and pronotum, superficial or vague on elytra; punctures very small on head and pronotum, absent on elytra.

Head: Widest at eyes; eyes convex; clypeus moderately excavated; clypeal line absent; antero-lateral margins not raised. Third antennal segment 1,6 times as long as 2nd, longer than 4th and 5th combined. Punctures very small, hardly visible.

Pronotum: 1,33 times as broad as head, somewhat broader than long ($W/L = 1,27$), very convex ($W/H = 1,37$). Punctures as small as those on head. Holotype: length 1,10 mm, width 1,40 mm, height 1,02 mm.

Elytra: Slightly narrower than pronotum, slightly broader than long ($W/L = 1,07$), moderately convex ($W/H = 1,77$); lateral outline with broadly rounded humeral angle; sutural striae absent. Microreticulation very superficial or vague on entire surface; puncturation absent, except for some very small punctures. Holotype: length 1,26 mm, width 1,35 mm, height 0,76 mm.



FIGS 193-200

Male hind femur of: 193, *Agathidium fuscum* n.sp.; 194, *A. lunatum* n.sp.; 195, *A. umbratum* n.sp.; 196, *A. fenestratum* n.sp.; 197, *A. asphaltinum* n.sp.; 198, *A. splendidulum* n.sp.; 199, *A. melanocephalum* n.sp.; 200, *A. chiaicum* n.sp.

Metathoracic wings absent. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines complete.

Legs: Male hind femora with sharp tooth (fig. 136). Tarsal formula: ♂ 5-5-4, ♀ 5-4-4.

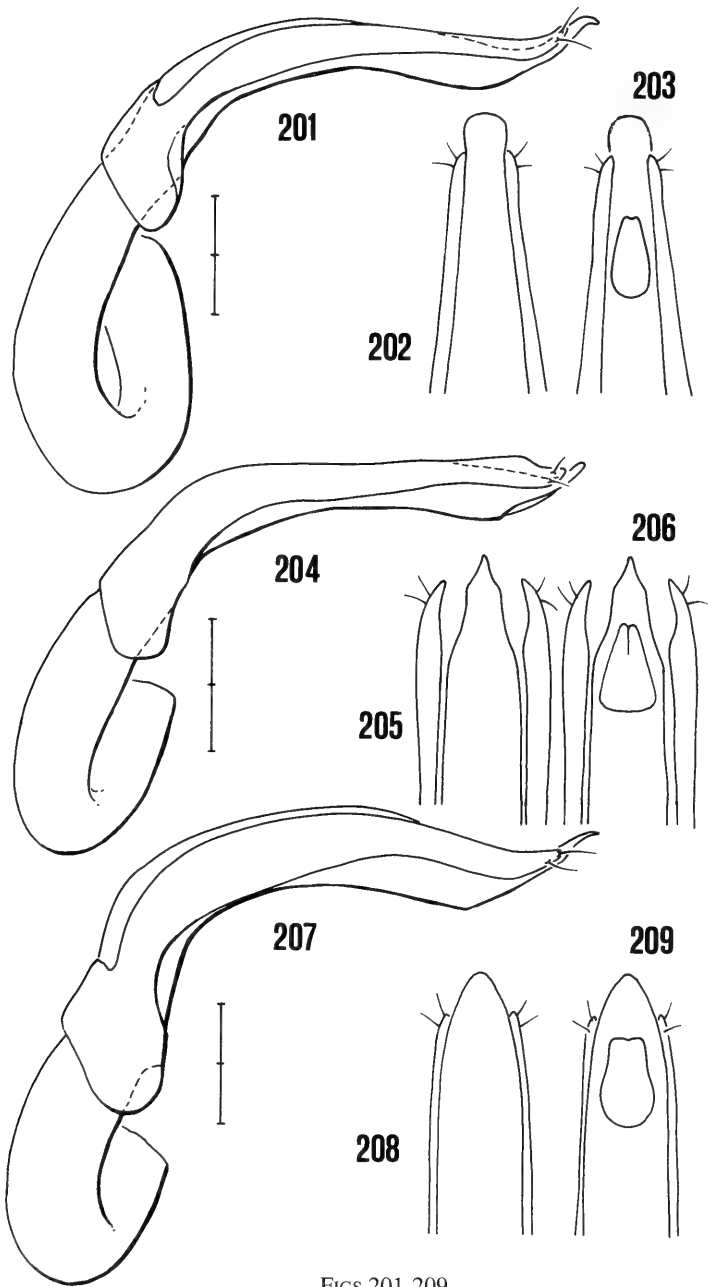
Male copulatory organ (figs 204-206): Aedeagus very slender, with hook-like proximal part, lateral margins parallel and then sinuously converging toward subacute apex, ventral piece split. Parameres stout, sinuously narrowing toward apex.

Spermatheca (fig. 184): Basal part pyriform, apical part elongate.

HOLOTYPE ♂: Chiai Hsien, Yushan N. P., Mun-Li Cliff, 1700 m, 27.IV.1990, in MHNG.

PARATYPES: Together with the holotype, 3♂ and 3♀ in MHNG, 2♀ in NMNT, 2♂ and 1♀ in AC; Nantou Hsien, Yushan N. P., Mun-Li Cliff, 2700 m, 13.V.1991, 2♂ and 1♀ in MHNG.

Discussion: See the discussion of *A. subalpinum*. *Agathidium inustum* n.sp. differs from *A. taichungense* n.sp. and *A. exoletum* n.sp. by the size and by the length ratio of 3rd/2nd antennal segments.



FIGS 201-209

Male copulatory organ (lateral view and dorsal/ventral view of its apex) of: 201-203, *Agathidium intricatum* n.sp.; 204-206, *A. inustum* n.sp.; 207-209, *A. taichungense* n.sp. Scales: 1 division = 0,1 mm.

Habitat: Original mixed coniferous and broad-leaved forest, moss, litter, rotting bark and wood around huge trees.

Distribution: Taiwan.

Agathidium (s.str.) taichungense n.sp.

Figs. 92, 137, 177, 185, 207-209

Length 3,4-3,6 mm (holotype ♂ 3,45 mm). Entire dorsum black, reddish-brown along the suture; venter reddish-brown; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on head and pronotum, superficial or vague on elytra; puncturation fine and sparse on head and pronotum, absent on elytra.

Head: Widest at eyes; eyes convex; clypeus moderately excavated; clypeal line absent; antero-lateral margins not raised. Third antennal segment 1,1 times as long as 2nd, as long as 4th and 5th combined (fig. 92). Punctures very small, hardly visible.

Pronotum: 1,3 times as broad as head, slightly broader than long ($W/L = 1,29$), very convex ($W/H = 1,45$). Dorsal and lateral outlines: fig. 177. Punctures as small as those on head. Holotype: length 1,16 mm, width 1,50 mm, height 1,03 mm.

Elytra: Narrower than pronotum, moderately broader than long ($W/L = 1,87$), moderately convex ($W/H = 1,62$); lateral outline with broadly rounded humeral angle; sutural striae absent. Microreticulation very superficial or vague; puncturation absent, except for some very small punctures. Holotype: length 1,60 mm, width 1,40 mm, height 0,86 mm.

Metathoracic wings absent. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines incomplete.

Legs: Male hind femora with sharp tooth (fig. 137). Tarsal formula: ♂ 5-5-4, ♀ 5-4-4.

Male copulatory organ (figs 207-209): Aedeagus slender, with hook-like proximal part, lateral margins parallel and then abruptly converging toward rounded apex, ventral piece slightly emarginate. Parameres stout, gently narrowing toward apex.

Spermatheca (fig. 185): Both basal and apical parts elongate; the basal part longer and larger.

HOLOTYPE ♂: Taichung Hsien, Hsuehshan, near Hsuehshan Tun-Feng, 3170 m, 7.V.1991, in MHNG.

PARATYPES: Together with the holotype, 1♂ and 1♀ in AC; same locality, near Hsuehshan Tun-Feng, 3170 m, 11.V.1991, 1♂ and 5♀ in MHNG, 2♀ in NMNT.

Discussion: See the discussion of *A. inustum*. *Agathidium taichungense* n.sp. is closely related to *A. exoletum* n.sp., from which it differs only by the shape of the pronotum and the elytra. Separation of these species must be based on the male copulatory organ.

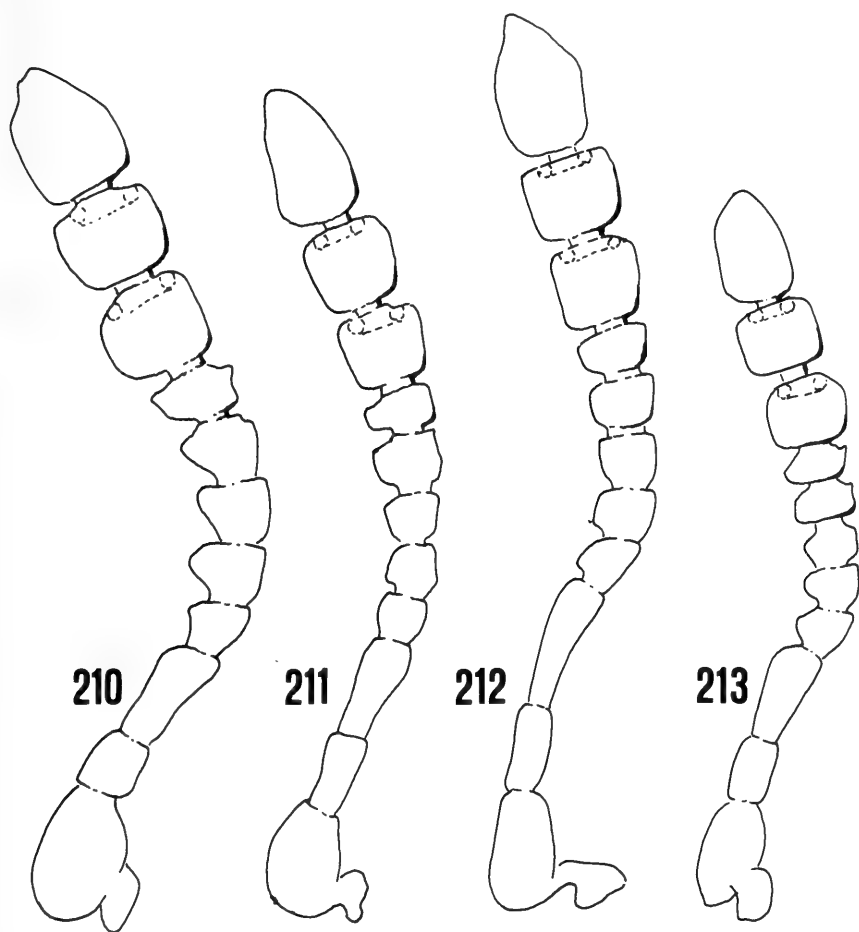
Habitat: Original coniferous forest on northern slope, dead vegetation, various debris and moss.

Distribution: Taiwan.

Agathidium (s.str.) exoletum n.sp.

Figs. 93, 138, 178, 186, 214-216

Length 3,3-3,4 mm (holotype ♂ 3,40 mm). Entire dorsum black; venter reddish-brown, paler at mesosternum; antennae uniformly testaceous; legs reddish-



FIGS 210-213

Antenna of: 210, *Agathidium fuscum* n.sp.; 211, *A. lunatum* n.sp.; 212, *A. umbratum* n.sp.; 213, *A. splendidulum* n.sp.

brown. Microreticulation absent on head and pronotum, superficial or vague on elytra; punctures very small on head, sparse on pronotum and elytra.

Head: Widest at eyes; eyes convex; clypeus moderately excavated; clypeal line absent; antero-lateral margins not raised. Third antennal segment 1,3 times as long as 2nd, as long as 4th and 5th combined (fig. 93); Hamann's organ: gutter without vesicle in both 9th and 10th antennal segments. Punctures very small, hardly visible.

Pronotum: 1,36 times as broad as head, moderately broader than long ($W/L = 1,46$), very convex ($W/H = 1,46$). Dorsal and lateral outlines: fig. 178. Punctures very small and sparse. Holotype: length 1,08 mm, width 1,58 mm, height 1,08 mm.

Elytra: As broad as pronotum, slightly broader than long ($W/L = 1,09$), little convex ($W/H = 2,25$); lateral outline with broadly rounded humeral angle; sutural striae absent. Microreticulation very superficial or vague; puncturation absent, except for some very small punctures. Holotype: length 1,45 mm, width 1,58 mm, height 0,70 mm.

Metathoracic wings absent. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines complete.

Legs: Male hind femora with a sharp distal tooth (fig. 138). Tarsal formula: ♂ 5-5-4, ♀ 5-4-4.

Male copulatory organ (figs 214-216): Aedeagus very slender, with hook-like proximal part, lateral margins gently converging toward subacute apex, ventral piece slightly emarginate. Parameres stout, with subapical enlargement.

Spermatheca (fig. 186): Basal part pyriform, apical part elongate.

HOLOTYPE ♂: Pingtung Hsien, Peitawushan, Kuai-Ku Hut, 2325 m, 21.V.1991, in MHNG.

PARATYPES: Together with the holotype, 1 ♀ in NMNT, 1 ♂ in AC; Kaohsiung Hsien, Tengchih, 1535 m, 23.IV.1990, 1 ♀ in MHNG.

Discussion: See the discussion of *A. taichungense*.

Habitats: Coniferous forest of *Taiwania cryptomeroides* fallen twigs, humus and various debris, mainly along fallen trees. Original broad-leaved forest, dead vegetation, fallen leaves and other debris.

Distribution: Taiwan.

Group: **dentatum**

Agathidium (s.str.) fuscum n.sp.

Figs. 179, 193, 210, 217-219

Length 4,10 mm (holotype ♂). Entire dorsum black; venter reddish-brown; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on entire dorsum; punctures very small on head and pronotum, nearly absent on elytra.

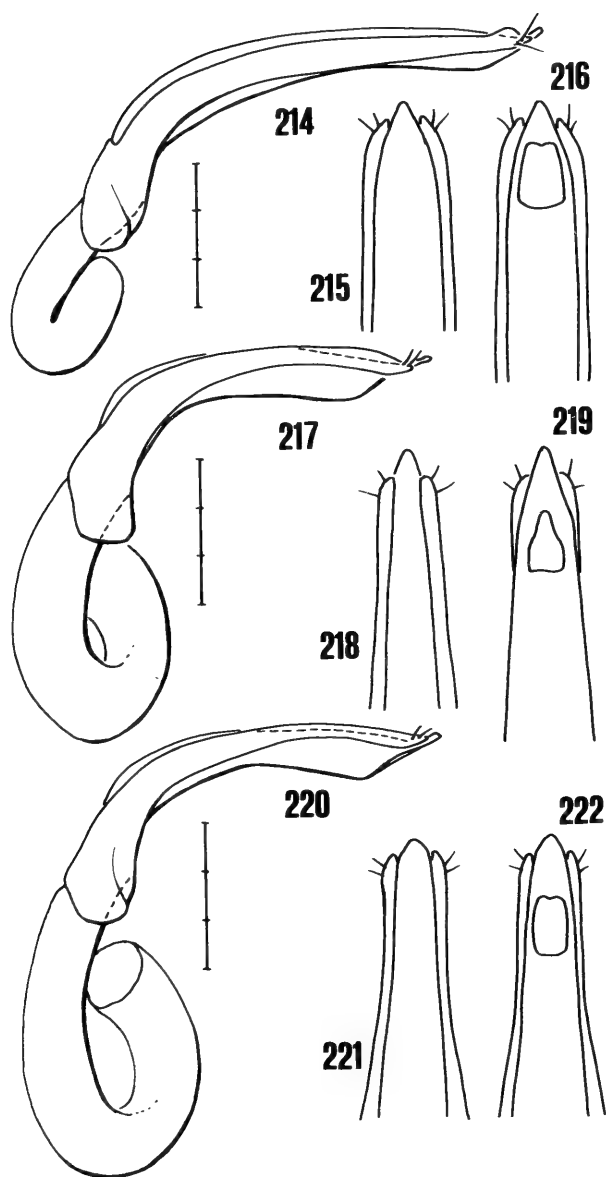
Head: Widest at eyes; eyes convex; clypeus sharply excavated; clypeal line absent; antero-lateral margins not raised. Third antennal segment 1,8 times as long as 2nd, as long as 4th and 5th combined (fig. 210); Hamann's organ: gutter without vesicle in both 9th and 10th antennal segments. Punctures very small, superficial, spaced from each other by 6-10 times their own diameter.

Pronotum: 1,3 times as broad as head, as broad as long, very convex ($W/H = 1,38$). Dorsal and lateral outlines: fig. 179. Punctures as small as those on head. Holotype: length 1,72 mm, width 1,83 mm, height 1,32 mm.

Elytra: Narrower than pronotum, moderately broader than long ($W/L = 1,06$), slightly convex ($W/H = 1,88$); lateral outline with broadly rounded humeral angle; sutural striae absent. Puncturation absent, except for some very small punctures. Holotype: length 1,65 mm, width 1,75 mm, height 0,93 mm.

Metathoracic wings absent. Meso- and metasternum: median carina absent, lateral lines absent, femoral lines complete.

Legs: Male hind femora with small subdistal tooth (fig. 193). Tarsal formula: ♂ 5-5-4, ♀ not known.



FIGS 214-222

Male copulatory organ (lateral view and dorsal/ventral view of its apex) of: 214-216, *Agathidium exoletum* n.sp.; 217-219, *A. fuscum* n.sp.; 220-222, *A. lunatum* n.sp. Scales: 1 division = 0,1 mm.

Male copulatory organ (figs 217-219): Aedeagus slender, with ring-like proximal part, lateral margins gently converging toward rounded apex, ventral piece not bifid. Parameres slender, gently narrowing toward apex.

HOLOTYPE ♂: Taoyuan Hsien, Takuanshan For., 1650 m, 17.IV.1990, in MHNG.

Discussion: Within the *dentatum* group, *Agathidium fuscum* n.sp. shares with *A. lunatum* n.sp., *A. umbratum* n.sp. and *A. fenestratum* n.sp. the large size in addition to numerous other external features; it differs from these species by the shape of the male hind femora, by the ratio of 3rd/2nd antennal segments, and by the width/length ratio of the pronotum.

Habitat: Original broad-leaved forest, moist debris and humus among the lush vegetation along a trail.

Distribution: Taiwan.

***Agathidium (s.str.) lunatum* n.sp.**

Figs. 180, 194, 211, 220-222

Length 4,0 mm (holotype ♂ 4,05 mm). Entire dorsum black, reddish-brown along the suture; venter reddish-brown; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on entire dorsum; punctures very small on head and pronotum, absent on elytra.

Head: Widest at eyes; eyes convex; clypeus moderately excavated; clypeal line absent; antero-lateral margins slightly raised. Third antennal segment 1,6 times as long as 2nd, shorter than 4th and 5th combined (fig. 211); Hamann's organ: gutter without vesicle in both 9th and 10th antennal segments. Punctures very small, superficial, spaced from each other by 5-10 times their own diameter.

Pronotum: 1,27 times as broad as head, slightly broader than long (W/L = 1,16), very convex (W/H = 1,31). Dorsal and lateral outlines: fig. 180. Punctures as small and sparse as those on head. Holotype: length 1,50 mm, width 1,75 mm, height 1,33 mm.

Elytra: As broad as pronotum, as broad as long, moderately convex (W/H = 1,78); lateral outline with broadly rounded humeral angle; sutural striae absent. Holotype: length 1,71 mm, width 1,75 mm, height 0,98 mm.

Metathoracic wings absent. Meso- and metasternum: median carina weak, lateral lines absent, femoral lines complete.

Legs: Male hind femora broadened at middle of their length (fig. 194). Tarsal formula: ♂ 5-5-4, ♀ not known.

Male copulatory organ (figs 220-222): Aedeagus slender, with ring-like proximal part, lateral margins gently converging toward rounded apex, ventral piece slightly emarginate. Parameres slender, gently narrowing toward apex.

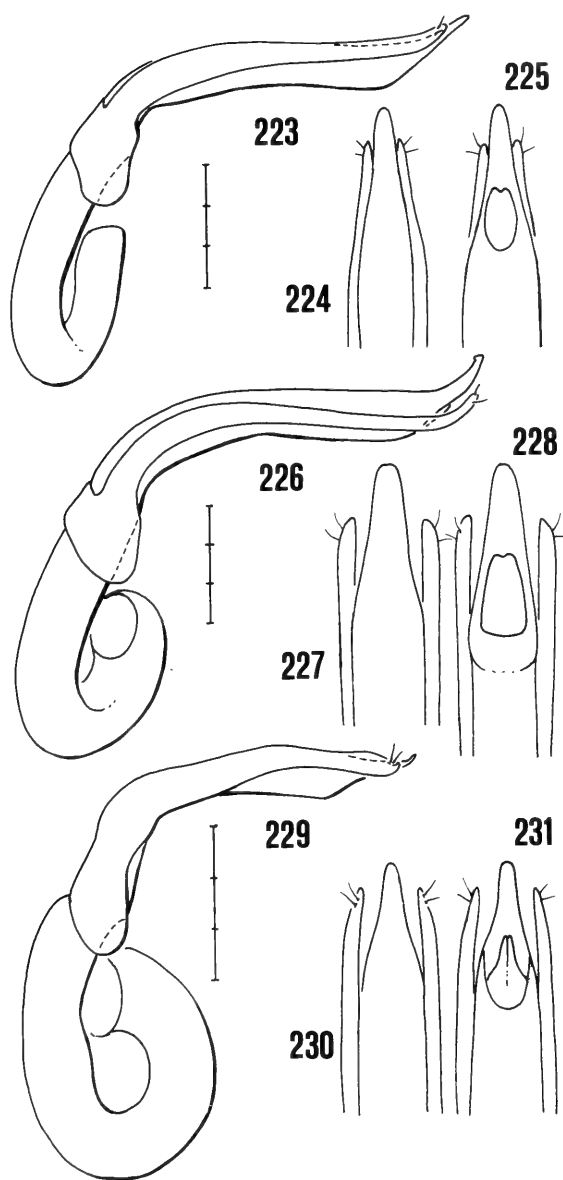
HOLOTYPE ♂: Pingtung Hsien, Peitawushan, Kuai-Ku Hut, 2325 m, 21.V.1991, in MHNG.

PARATYPE: Together with the holotype, 1 ♂ in AC.

Discussion: See the discussion of *A. fuscum*.

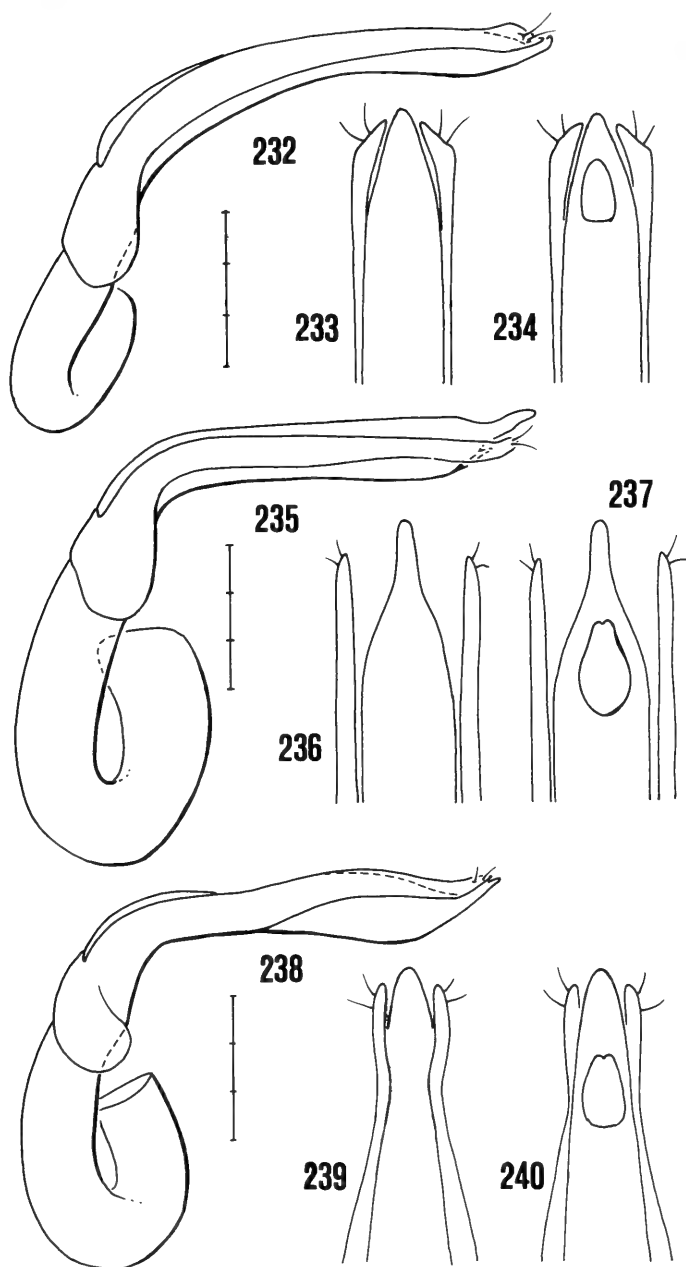
Habitat: Original broad-leaved forest; dead vegetation, fallen leaves and other debris.

Distribution: Taiwan.



FIGS 223-231

Male copulatory organ (lateral view and dorsal/ventral view of its apex) of: 223-225, *Agathidium umbratum* n.sp.; 226-228, *A. fenestratum* n.sp.; 229-231, *A. asphaltinum* n.sp.
Scales: 1 division = 0,1 mm.



FIGS 232-240

Male copulatory organ (lateral view and dorsal/ventral view of its apex) of: 232-234, *Agathidium splendidulum* n.sp.; 235-237, *A. melanocephalum* n.sp.; 238-240, *A. chiaicum* n.sp.
Scales: 1 division = 0,1 mm.

Agathidium (s.str.) umbratum n.sp.

Figs. 187, 188, 195, 212, 223-225

Length 4,15 mm (holotype ♂). Entire dorsum black; venter dark reddish-brown; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on entire dorsum; punctures very small on head and pronotum, absent on elytra.

Head: Widest at eyes (fig. 187); eyes convex; clypeus sharply excavated; clypeal line absent; antero-lateral margins not raised. Third antennal segment 1,5 times as long as 2nd, shorter than 4th and 5th combined (fig. 212); Hamann's organ: gutter without vesicle in both 9th and 10th antennal segments. Punctures very small, hardly visible.

Pronotum: 1,48 times as broad as head, slightly broader than long ($W/L = 1,24$), very convex ($W/H = 1,43$). Dorsal and lateral outlines: fig. 188. Punctures as small as those on head, sparser. Holotype: length 1,61 mm, width 2,00 mm, height 1,40 mm.

Elytra: As broad as pronotum, moderately broader than long ($W/L = 1,21$), little convex ($W/H = 2,22$); lateral outline with broadly rounded humeral angle; sutural striae absent. Punctuation absent, except for some very small punctures. Holotype: length 1,65 mm, width 2,00 mm, height 0,90 mm.

Metathoracic wings absent. Meso- and metasternum: median carina absent, lateral lines absent, femoral lines incomplete.

Legs: Male hind femora with sharp tooth (fig. 195). Tarsal formula: ♂ 5-5-4, ♀ not known.

Male copulatory organ (figs 223-225): Aedeagus very slender, with hook-like proximal part, lateral margins sinuously converging toward rounded apex, ventral piece slightly emarginate. Parameres stout, gently narrowing toward apex.

HOLOTYPE ♂: Taoyuan Hsien, Takuanshan For., 1650 m, 17.IV.1990, in MHNG.

Discussion: See the discussion of *A. fuscum*. *Agathidium umbratum* n.sp. shares with *A. fenestratum* n.sp. the shape of the male hind femora; it differs by the shape of the head and elytra.

Habitat: Original broad-leaved forest, moist debris and humus among the lush vegetation along a trail.

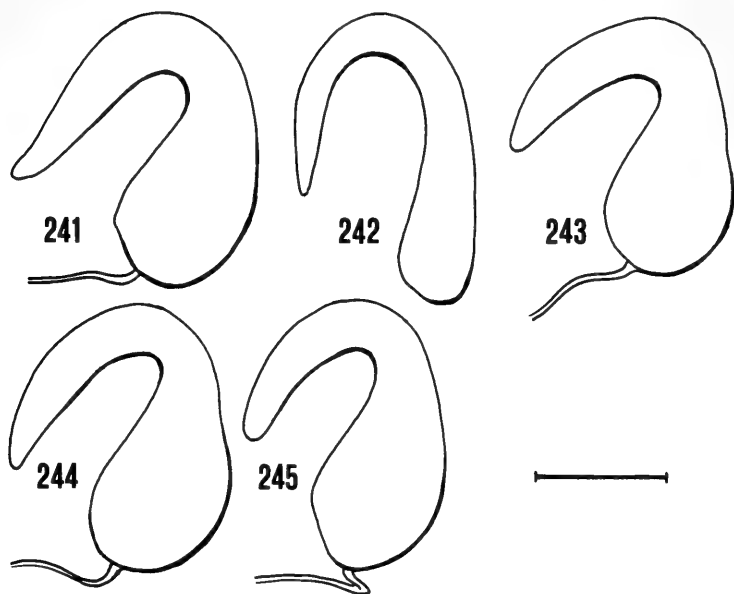
Distribution: Taiwan.

Agathidium (s.str.) fenestratum n.sp.

Figs. 189, 190, 196, 226-228, 241

Length 4,0-4,1 mm (holotype ♂ 4,05 mm). Entire dorsum black, reddish-brown along the suture; venter dark reddish-brown, paler at mesosternum; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on entire dorsum; punctuation fine and sparse on entire dorsum.

Head: Widest at eyes (fig. 189); eyes flattened; clypeus moderately excavated; clypeal line absent; antero-lateral margins slightly raised. Third antennal segment 1,5 times as long as 2nd, shorter than 4th and 5th combined. Punctures small, moderately impressed, spaced from each other by 5-10 times their own diameter.



FIGS 241-245

Spermatheca of: 241, *Agathidium fenestratum* n.sp.; 242, *A. asphaltinum* n.sp.; 243, *A. splendidulum* n.sp.; 244, *A. melanocephalum* n.sp.; 245, *A. chiaicum* n.sp. Scale: 1 division = 0,1 mm.

Pronotum: 1,3 times as broad as head, slightly broader than long ($W/L = 1,25$), very convex ($W/H = 1,46$). Dorsal and lateral outlines: fig. 190. Punctures somewhat larger and deeper than at head, spaced from each other by 1-10 times their own diameter. Holotype: length 1,46 mm, width 1,83 mm, height 1,25 mm.

Elytra: As broad as pronotum, as broad as long, moderately convex ($W/H = 1,8$); lateral outline with broadly rounded humeral angle; sutural striae absent. Punctuation absent, except for some punctures similar to those of head. Holotype: length 1,72 mm, width 1,80 mm, height 1,00 mm.

Metathoracic wings absent. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines complete.

Legs: Male hind femora with sharp tooth (fig. 196). Tarsal formula: ♂ 5-5-4, ♀ 5-4-4.

Male copulatory organ (figs 226-228): Aedeagus very slender, with ring-like proximal part, lateral margins sinuously converging toward rounded apex, ventral piece slightly emarginate. Parameres slender, gently narrowing toward apex.

Spermatheca (fig. 241): Basal part pyriform, apical part elongate.

HOLOTYPE ♂: Chiai Hsien, Yushan N. P., Mun-Li Cliff, 1700 m, 27.IV.1990, in MHNG.

Paratypes: Together with the holotype, 1 ♀ in NMNT, 1 ♂ and 1 ♀ in AC.

Discussion: See the discussion of *A. umbratum*.

Habitat: Original mixed coniferous and broad-leaved forest, moss, litter, rotting bark and wood around huge trees.

Distribution: Taiwan.

Agathidium (s.str.) asphaltinum n.sp.

Figs. 197, 229-231, 242

Length 3,0-3,3 mm (holotype ♂ 3,05 mm). Entire dorsum black or reddish-brown; venter reddish-brown, paler at mesosternum; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on head and pronotum, vague on elytra; punctures very small on head and pronotum, absent on elytra.

Head: Widest at eyes; eyes convex; clypeus sharply excavated; clypeal line absent; antero-lateral margins slightly raised. Third antennal segment as long as 2nd, as long as 4th and 5th combined. Punctures very small, hardly visible.

Pronotum: 1,24 times as broad as head, slightly broader than long (W/L = 1,39), very convex (W/H = 1,4). Punctures as small as those on head. Holotype: length 1,05 mm, width 1,46 mm, height 1,04 mm.

Elytra: Narrower than pronotum, as broad as long, moderately convex (W/H = 1,78); lateral outline with broadly rounded humeral angle; sutural striae absent. Only traces of microreticulation. Holotype: length 1,30 mm, width 1,36 mm, height 0,76 mm.

Metathoracic wings absent. Meso- and metasternum: median carina weak, lateral lines absent, femoral lines incomplete.

Legs: Male hind femora with small subdistal tooth (fig. 197). Tarsal formula: ♂ 5-5-4, ♀ 5-4-4.

Male copulatory organ (figs 229-231): Aedeagus stout, with ring-like proximal part, lateral margins sinuously converging toward rounded apex, ventral piece deeply split. Parameres stout, gently narrowing toward apex.

Spermatheca (fig. 242): Both basal and apical parts elongate; basal part longer and larger.

HOLOTYPE ♂: Kaohsiung Hsien, Tengchih, 1610 m, 24.IV.1990, in MHNG.

PARATYPE: Together with the holotype, 1 ♀ in AC.

Discussion: Within the *dentatum* group, *Agathidium asphaltinum* n.sp. is closely related to *A. splendidulum* n.sp., *A. melanocephalum* n.sp. and *A. chiaicum* n.sp. due to numerous external features; diagnostic characters are the shape of the male hind femora, the ratio of 3rd/2nd antennal segments and the width/length ratio of the pronotum.

Habitat: Large clearing in a broad-leaved forest, dead vegetation and humus, rotting bark and wood along fallen trees and stumps.

Distribution: Taiwan.

Agathidium (s.str.) splendidulum n.sp.

Figs. 191, 198, 213, 232-234, 243

Length 3,6-3,7 mm (holotype ♂ 3,65 mm). Entire dorsum black, reddish-brown along the suture; venter reddish-brown; antennae uniformly testaceous; legs

reddish-brown. Microreticulation absent on entire dorsum; puncturation fine and sparse on entire dorsum.

Head: Widest at eyes; eyes convex; clypeus moderately excavated; clypeal line absent; antero-lateral margins not raised. Third antennal segment 1,5 times as long as 2nd, shorter than 4th and 5th combined (fig. 213); Hamann's organ: gutter without vesicle in both 9th and 10th antennal segments. Punctures very small, hardly visible.

Pronotum: 1,26 times as broad as head, slightly broader than long ($W/L = 1,15$), very convex ($W/H = 1,29$). Dorsal and lateral outlines: fig. 191. Punctures as small as those on head. Holotype: length 1,40 mm, width 1,62 mm, height 1,25 mm.

Elytra: Narrower than pronotum, as broad as long, moderately convex ($W/H = 1,66$); lateral outline with broadly rounded humeral angle; sutural striae absent. Punctures larger than at head, very superficial, spaced from each other by 1-10 times their own diameter. Holotype: length 1,53 mm, width 1,50 mm, height 0,90 mm.

Metathoracic wings absent. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines incomplete.

Legs: Male hind femora with very sharp tooth (fig. 198). Tarsal formula: ♂ 5-5-4, ♀ 5-4-4.

Male copulatory organ (figs 232-234): Aedeagus very slender, with hook-like proximal part, lateral margins gently converging toward rounded apex, ventral piece slightly emarginate. Parameres slender, with subapical enlargement.

Spermatheca (fig. 243): Basal part pyriform, apical part elongate.

HOLOTYPE ♂: Nantou Hsien, Meifeng, 2130 m, 13.V.1991, in MHNG.

PARATYPES: Together with the holotype, 1 ♀ in MHNG, 1 ♀ in NMNT; same locality, 2130 m, 3.V.1991, 1 ♂ in AC.

Discussion: See the discussion of *A. asphaltinum*.

Habitats: Original broad-leaved forest; lush vegetation, debris and humus along a road; moss on large fallen trees and debris along them.

Distribution: Taiwan.

Agathidium (s.str.) melanocephalum n.sp.

Figs. 192, 199, 235-237, 244

Length 3,3-3,8 mm (holotype ♂ 3,85 mm). Entire dorsum black; venter reddish-brown; antennae uniformly testaceous; legs reddish-brown. Microreticulation on entire dorsum; punctures very small on entire dorsum.

Head: Widest at eyes; eyes convex; clypeus moderately excavated; clypeal line absent; antero-lateral margins raised. Third antennal segment 1,3 times as long as 2nd, shorter than 4th and 5th combined. Punctures very small, hardly visible.

Pronotum: 1,24 times as broad as head, slightly broader than long ($W/L = 1,28$), moderately convex ($W/H = 1,5$). Dorsal and lateral outlines: fig. 192. Punctures as small and sparse as those on head. Holotype: length 1,40 mm, width 1,80 mm, height 1,20 mm.

Elytra: Narrower than pronotum, as broad as long, moderately convex ($W/H = 1,77$); lateral outline with broadly rounded humeral angle; sutural striae absent. Punctures as small as those on head. Holotype: length 1,65 mm, width 1,70 mm, height 0,96 mm.

Metathoracic wings absent. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines incomplete.

Legs: Male hind femora with sharp tooth (fig. 199). Tarsal formula: ♂ 5-5-4, ♀ 5-4-4.

Male copulatory organ (figs 235-237): Aedeagus slender, with hook-like proximal part, lateral margins parallel and then abruptly converging toward rounded apex, ventral piece split. Parameres slender, gently narrowing toward apex.

Spermatheca (fig. 244): Basal part pyriform, apical part elongate.

HOLOTYPE ♂: Chiai Hsien, Yushan N. P., Mun-Li Cliff, 1700 m, 27.IV.1990, in MHNG.

PARATYPES: Together with the holotype, 2♂ and 2♀ in MHNG, 1♂ and 1♀ in AC; Nantou Hsien, Yushan N. P., Mun-Li Cliff, 2700 m, 13.V.1991, 2♂ and 1♀ in MHNG; same locality, Mun-Li Cliff, 2700 m, 18.V.1991, 1♂ and 1♀ in MHNG, 2♀ in NMNT, 1♂ and 1♀ in AC; Hualien Hsien, Taroko N. P., ridge SE Nanhushi Hut, 2700 m, 11.V.1990, 1♂ in MHNG.

Discussion: See the discussion of *A. asphaltinum*. *Agathidium melanocephalum* n.sp. is closely related to *A. chiaicum* n.sp.; it may be distinguished from it merely by the male copulatory organ.

Habitats: Original mixed coniferous and broad-leaved forest. Original coniferous forest, rotting bark and wood, humus, moss and old mushrooms on and around fallen trees.

Distribution: Taiwan.

***Agathidium* (s.str.) *chiaicum* n.sp.**

Figs. 200, 238-240, 245

Length 3,1-3,5 mm (holotype ♂ 3,40 mm). Entire dorsum black; venter reddish-brown; antennae uniformly testaceous; legs reddish-brown. Microreticulation absent on head and pronotum, vague on elytra; punctures very small, nearly absent on elytra.

Head: Widest at eyes; eyes convex; clypeus moderately excavated; clypeal line absent; antero-lateral margins slightly raised. Third antennal segment 1,2 times as long as 2nd, shorter than 4th and 5th combined. Punctures very small, hardly visible.

Pronotum: 1,29 times as broad as head, slightly broader than long (W/L = 1,34), moderately convex (W/H = 1,55). Punctures as small as those on head. Holotype: length 1,15 mm, width 1,55 mm, height 1,00 mm.

Elytra: As broad as pronotum, as broad as long, moderately convex (W/H = 1,8); lateral outline with broadly rounded humeral angle; sutural striae absent. Only traces of microreticulation; puncturation absent, except for some very small punctures. Holotype: length 1,55 mm, width 1,55 mm, height 0,85 mm.

Metathoracic wings absent. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines incomplete.

Legs: Male hind femora with sharp tooth (fig. 200). Tarsal formula: ♂ 5-5-4, ♀ 5-4-4.

Male copulatory organ (figs 238-240): Aedeagus slender, with hook-like proximal part, lateral margins gently converging toward rounded apex, ventral piece split. Parameres stout, gently narrowing toward apex.

Spermatheca (fig. 245): Basal part pyriform, apical part elongate.

HOLOTYPE ♂: Chia Hsien, Yushan N. P., Mun-Li Cliff, 1700 m, 27.IV.1990, in MHNG.

PARATYPES: Together with the holotype, 5 ♂ and 3 ♀ in MHNG, 1 ♂ and 1 ♀ in NMNT, 1 ♂ and 1 ♀ in AC; Nantou Hsien, Yushan N. P., Mun-Li Cliff, 2700 m, 13.V.1991, 2 ♂ and 1 ♀ in MHNG, 1 ♂ and 1 ♀ in AC.

Discussion: See the discussion of *A. asphaltinum* and *A. melanocephalum*.

Habitat: Original mixed coniferous and broad-leaved forest, moss, litter, rotting bark and wood around huge trees.

Distribution: Taiwan.

Subg. *Microceble* Angelini & De Marzo, 1986

Group: *grouvellei*

Agathidium (Microceble) klapperichi Ang. & Dmz.

Agathidium (Microceble) klapperichi Angelini & De Marzo, 1985, Entomologica, 19: 41 (s.str.); 1986a, Rev. suisse Zool., 93 (2): 454.

Material: Kaohsiung Hsien, Tengchih, 1580 m, 24.IV.1990, 2 ♀ in MHNG; same locality, 1610 m, 24.IV.1990, 2 ♂ and 2 ♀ in MHNG, 1 ♂ and 1 ♀ in NMNT, 1 ♂ and 1 ♀ in AC.

Habitat: Large clearing in a broad-leaved forest, dead vegetation and humus, rotting bark and wood along fallen trees and stumps.

Distribution: Taiwan.

Agathidium (Microceble) amictum n.sp.

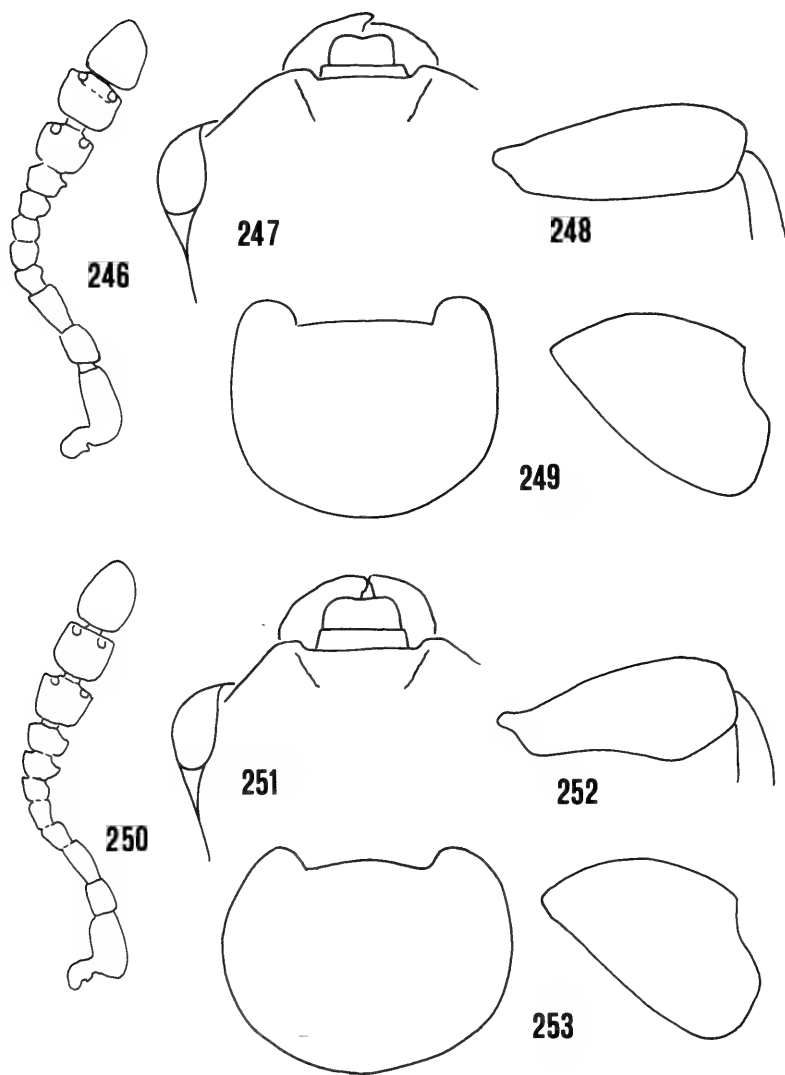
Figs. 246-249, 254-257

Length 2,9-3,2 mm (holotype ♂ 2,90 mm). Entire dorsum reddish-brown, sometimes paler around the border pronotum-elytra; venter reddish-brown, paler at mesosternum; antennae testaceous, darker at segments 7-10; legs reddish-brown. Head striolate, microreticulation superficial or vague on pronotum and elytra; puncturation sparse on head, nearly absent on pronotum and elytra.

Head: Widest at eyes (fig. 247); eyes very convex; clypeus moderately excavated; a short groove and a pit at each side of clypeus; antero-lateral margins raised. Third antennal segment 1,2 times as long as 2nd, shorter than 4th and 5th combined (fig. 246); Hamann's organ: gutter without vesicle in both 9th and 10th antennal segments. Whole surface striolate. Punctures small, superficial, spaced from each other by 1-10 times their own diameter.

Pronotum: 1,84 times as broad as head, moderately broader than long (W/L = 1,42), moderately convex (W/H = 1,51). Dorsal and lateral outlines: fig. 249. Microreticulation superficial on entire surface; punctures small, superficial, spaced from each other by 3-20 times their own diameter. Holotype: length 1,00 mm, width 1,42 mm, height 0,94 mm.

Elytra: As broad as pronotum, as broad as long, moderately convex (W/H = 1,67); lateral outline with broadly rounded humeral angle; sutural striae absent.



FIGS 246-253

Antenna, head, male hind femur and pronotum (dorsal and lateral view) of: 246-249, *Agathidium amictum* n.sp.; 250-253, *A. venustum* n.sp.

Microreticulation superficial or vague; puncturation absent, except for some very small punctures. Holotype: length 1,35 mm, width 1,42 mm, height 0,85 mm.

Metathoracic wings present. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines incomplete.

Legs: Male hind femora broadened distally (fig. 248). Tarsal formula: ♂ 5-5-4, ♀ 5-4-4.

Male copulatory organ (figs 254-256): Aedeagus stout, with proximal part simple, apex deeply excavated, with median protuberance at apex, ventral piece deeply bifid. Parameres very large at base, abruptly tapered at middle of their length.

Spermatheca (fig. 257): Basal part pyriform, apical part elongate.

HOLOTYPE ♂: Kaohsiung Hsien, Tengchih, 1610 m, 24.IV.1990, in MHNG.

PARATYPES: Together with the holotype, 1 ♂ and 2 ♀ in MHNG, 1 ♂ and 1 ♀ in NMNT, 1 ♂ and 1 ♀ in AC; same locality, 1700-1800 m, 24.IV.1990, 1 ♀ in MHNG; Taichung Hsien, Wufeng, 100-200 m, 14.IV.1990, 1 ♀ in MHNG, 1 ♂ in AC; same locality, 100 m, 15.IV.1990, 2 ♀ in MHNG; Nantou Hsien, Fengnan, 700 m, 22.IV.1990, 1 ♀ in MHNG.

Discussion: *Agathidium amictum* n.sp. shares with *A. klapperichi* Ang. & Dmz. (1985: 41, Taiwan) and *A. puncticolle* Cooter (1984: 70, Taiwan, Philippines) the characters of the *grouvellei* group: the striolate head and the presence of grooves at the sides of clypeus; it differs from the former by having the entire head striolate and the pronotum microreticulate, and from the latter by the coloration of the antennae and by the shape of the aedeagus; if compared with the other species of the *grouvellei* group of SE Asia, *A. amictum* exhibits a remarkable affinity to *A. argutum* Ang. & Dmz. (1993: 470, Sabah), even in the male copulatory organ; however, the spermatheca is somewhat different.

Habitats: Large clearing in a broad-leaved forest, dead vegetation and humus, rotting bark and wood along fallen trees and stumps. Plum orchard, piles of rotting plum twigs and leaves. Secondary subtropical broad-leaved forest mixed with bamboo growths, litter.

Distribution: Taiwan.

Group: andrewesi

Agathidium (Microcele) taiwanense Ang. & Dmz.

Agathidium (Microcele) taiwanense Angelini & De Marzo, 1985, Entomologica, 19: 42 (s.str.); 1986, Rev. suisse Zool., 93: 454.

M a t e r i a l: Pingtung Hsien, Peitawushan, trail at 2000 m, 23.V.1991, 1 ♂ in MHNG.

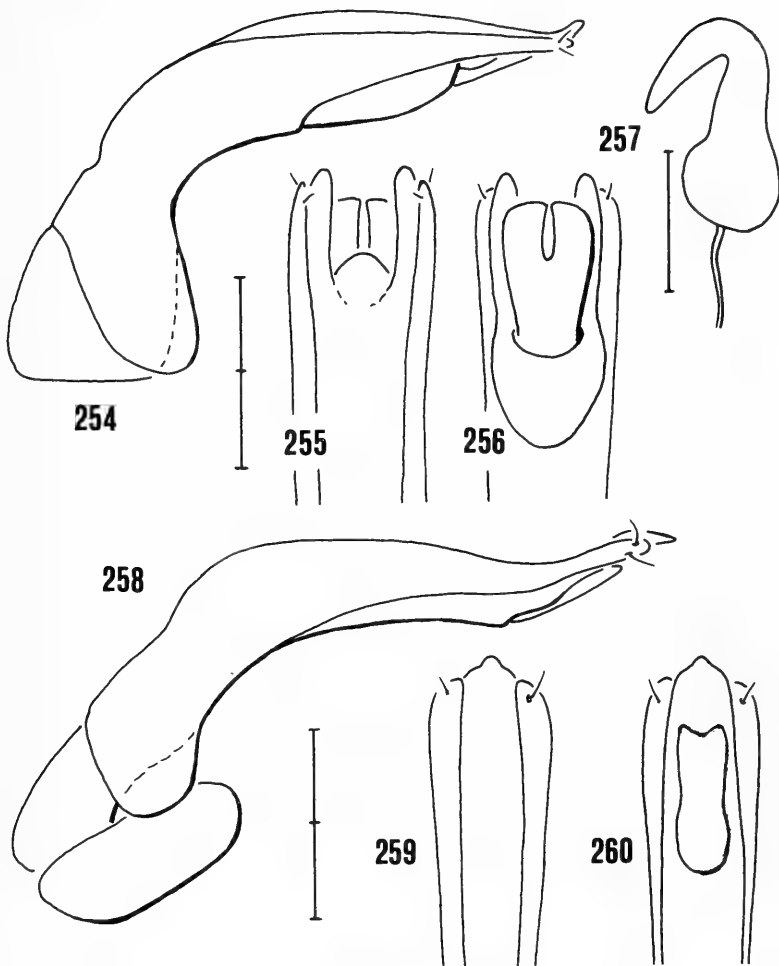
Habitat: Original broad-leaved forest, lush undergrowth along a trail, plant debris, litter and dead vegetation.

Distribution: Taiwan.

Agathidium (Microcele) venustum n.sp.

Figs. 250-253, 258-260

Length 3,0 mm (holotype ♂). Entire dorsum reddish-brown; antennae testaceous, darker at segments 9-10; legs reddish-brown. Microreticulation absent, except



FIGS 254-260

Male copulatory organ (lateral view and dorsal/ventral view of its apex) and spermatheca of: 254-257, *Agathidium amictum* n.sp.; 258-260, *A. venustum* n.sp. Scales: 1 division = 0,1 mm.

for traces on head and elytra; puncturation fine on head and pronotum, nearly absent on elytra.

Head: Widest at eyes (fig. 251); eyes very convex; clypeus slightly excavated; a short groove and a pit at each side of clypeus; antero-lateral margins raised. Third antennal segment 1,3 times as long as 2nd, shorter than 4th and 5th combined (fig. 250); Hamann's organ: gutter without vesicle in both 9th and 10th antennal segments.

Only traces of microreticulation. Punctures small, impressed, spaced from each other by 5-10 times their own diameter.

Pronotum: 1,87 times as broad as head, moderately broader than long ($W/L = 1,42$), moderately convex ($W/H = 1,52$). Dorsal and lateral outlines: fig. 253. Punctures somewhat smaller and more superficial than at head, spaced from each other by 0,5-20 times their own diameter. Holotype: length 1,00 mm, width 1,42 mm, height 0,93 mm.

Elytra: Narrower than pronotum, as broad as long, moderately convex ($W/H = 1,64$); lateral outline with broadly rounded humeral angle; sutural striae absent. Microreticulation absent or vague; puncturation absent, except for some very small punctures. Holotype: length 1,40 mm, width 1,35 mm, height 0,82 mm.

Metathoracic wings present. Meso- and metasternum: median carina raised, lateral lines absent, femoral lines incomplete.

Legs: Male hind femora broadened distally (fig. 252). Tarsal formula: ♂ 5-5-4, ♀ not known.

Male copulatory organ (figs 258-260): Aedeagus slender, with spiralled proximal part, lateral margins subparallel and then abruptly converging toward rounded apex, ventral piece slender and excavated. Parameres stout, gently narrowing toward apex.

HOLOTYPE ♂: Taichung Hsien, Wufeng, 100-200 m, 14.IV.1990, in MHNG.

Discussion: *Agathidium venustum* n.sp. is included in the *andrewesi* group due to the possession of clypeal grooves and the not striolate head; it differs from the only other species of *andrewesi* group known from Taiwan, *A. taiwanense* Ang. & Dmz. (1985: 42) by the ratio of 3rd/2nd antennal segments, by the coloration of antenna and by the shape of the aedeagus.

Habitat: Secondary subtropical broad-leaved forest mixed with bamboo growths.

Distribution: Taiwan.

REMARKS

Due to the insular and mountainous nature of Taiwan, the Agathidiini Fauna is characterized by the overwhelming of the endemic species (50 out 52). Non-endemic species are *Agathidium formosum* Ang. & Dmz., already known from Thailand, and *A. puncticolle* Cooter, known also from the Philippines and Sabah. Since some new species were found in single localities and/or in single specimens, we think that many additional new species likely occur in Taiwan.

As shown in table 1, the Fauna of Taiwan exhibits certain chorological features that are intermediate between those of the Palearctic and Oriental regions, as it is documented by the occurrence of:

I) the genus *Cyrtoplastus*, which was known so far only from the Palearctic region;

II) the subg. *Cyphoceble*, which is widely distributed in the Palearctic region but it is apparently rare in the Oriental region, being known only from the Himalaya so far;

III) the genus *Anisotoma*, which is typical of the Palearctic region;

IV) the genus *Afroagathidium*, which occurs in both the Oriental and Aethiopic regions, but is absent from the Palearctic region;

V) some subgeneric taxa of *Agathidium*, which are typical of the Oriental region, i.e., the *madurensis*-group and the subg. *Microceble*, both poorly represented in the Palearctic region, and the subg. *Macroceble* that is exclusive of the Oriental region.

As we have repeatedly emphasized in the chapters "Discussion", the identification of many species must be based on the male copulatory organ, because

TAB. 1

Number of species of the different taxa of Agathidiini known from Taiwan, compared with that of the other mentioned regions. The count includes some new species from China described in other papers in press.

taxa	number of known species from			
	Tai Wan	Nepal	Oriental R.	Palearctic R.
<i>Anisotoma</i>	1	2	6	21
<i>Amphicyllis</i>				2
<i>Afroagathidium</i>	1		2	
<i>Liodopria</i>	1	1	5	2
<i>Cyrtoplastus</i>	1		1	7
<i>Sphaeroliodes</i>				2
<i>Stetholiodes</i>		3	6	3
<i>Agathidium</i> (total)	48	129	329	163
subg. <i>Cyphoceble</i>	3	1	4	13
subg. <i>Neoceble</i>	5	5	14	73
<i>varians</i> group		1	1	23
<i>nigripennis</i> group	2	4	8	33
<i>marginatum</i> group	1		1	12
<i>canariense</i> group	2		4	5
subg. <i>Agathidium</i> s.str.	34	95	187	74
<i>madurensis</i> group	4	9	42	2
<i>seminulum</i> group	1	29	34	20
<i>atrum</i> group		7	15	6
<i>laevigatum</i> group	21	32	56	21
<i>dentatum</i> group	8	18	40	25
subg. <i>Microceble</i>	5	12	90	2
<i>maculatum</i> group			20	1
<i>grouvellei</i> group	3	8	42	
<i>andrewesi</i> group	2	4	28	1
subg. <i>Euryceble</i>			4	
subg. <i>Chaetoceble</i>				1
subg. <i>Macroceble</i>	1	16	30	
Agathidiini (total)	52	135	349	200

of the general uniformity of the other characters, including, in some instances, also the shape of the spermatheca. This difficulty arises also from some sentences in the key and is particularly sharp among the 18 species of the *laevigatum*-group. In these species we realize to be: I) microreticulation always very weak or vague (this is a rare feature within *Agathidium*); II) dorsal puncturation consisting of very small punctures on head and pronotum and absent on elytra of most species; III) tarsal formula constant (σ 5-5-4, φ 5-4-4); IV) colour of antennae constant; V) ratio of 3rd/2nd antennal segments constant (1,2) in as many as 8 species; VI) body length ranging from 2,4 and 3,7, except in a single 4,1 mm long species; VII) mesosternal carina lacking in one species only; VIII) lateral lines of mesosternum constantly absent; IX) metathoracic wings always absent.

An interesting reduction in the number of the antennal segments was found in *Anisotoma smetanai* n.sp. This feature was previously known in *Liodopria wallacei* (Angelini & Cooter, 1993: 67).

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Description of a new species of the genus *Astyanax* (Characiformes: Characidae) from the rio Araguaia basin, Brazil.

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Description of a new species of the genus *Astyanax* (Characiformes: Characidae) from the rio Araguaia basin, Brazil. - *Astyanax kullanderi* sp.n. is described from the upper rio Araguaia basin, central Brazil. It seems to be closely related to *A. validus* Géry, Planquette & Le Bail and *A. superbis* Myers by the common apomorphic colour pattern, and distinguished from them by a combination of characters involving number of anal fin rays, lateral line scales, and predorsal scales and gill-rakers, and absence of maxillary teeth.

Key-words: Pisces - Characidae - *Astyanax* n. sp. - Brazil.

INTRODUCTION

Astyanax Baird & Girard is a speciose genus, containing about 60 species occurring between southern United States and central Argentina (EIGENMANN 1917; GÉRY 1978). Although some species are currently poorly diagnosed and taxonomical problems involving widespread species (probably species complex) such as *A. fasciatus* (Cuvier) and *A. bimaculatus* (Linnaeus) are not solved, most species may be easily recognized on the basis of teeth morphology and number, colour pattern and meristics. In the present paper, a new species from the upper rio Araguaia basin in Mato Grosso, central Brazil, is described.

MATERIAL AND METHODS

Methods for counts of fin-rays, scales, vertebrae, and gill-rakers follow FINK & WEITZMAN (1974). Measurements are made according to FINK & WEITZMAN (1974), except for: body depth, vertical measure immediately anterior to dorsal fin origin; body width, transverse measure immediately in front dorsal fin base; head depth, vertical

measure through the posterior edge of opercular bone; and, head width, the largest transverse length crossing the head. Tooth and dental cusp counts are made from the medial to the distal portion of jaw bones. Cleared and counterstained specimens prepared according to TAYLOR & VAN DYKE (1985). Abbreviations for institutions are: MHNG – Muséum d'histoire naturelle, Genève; MNRJ – Museu Nacional do Rio de Janeiro; MZUSP – Museu de Zoologia da Universidade de São Paulo; NRM – Naturhistoriska Riksmuseet, Stockholm, and UFRJ – Universidade do Rio de Janeiro.

***Astyanax kullanderi* sp.n.**

(Fig. 1-2)

HOLOTYPE. MNRJ 12427, 57.2 mm SL; Brazil: Estado de Mato Grosso, stream tributary of rio Perdidos, rio das Mortes drainage, close to the road BR-070, about 10 km W of Primavera do Leste, 15°32'S, 54°18'W; S.O. Kullander, A. Hoggeborn-Kullander, K. Tanizaki & M.T. Lacerda, 19.X.1989.

PARATYPES. UFRJ 1290, 7 ex., 35.6-64.4 mm SL; MHNG 2542.17, 3 ex., 37.4-55.3 mm SL; NRM uncatalogued, 4 ex., 34.7-55.2 mm SL; MNRJ 12428, 5 ex., 36.4-56.6 mm SL; MZUSP 45288, 3 ex., 40.7-51.3 mm SL; UFRJ 1291, 4 stained and cleared ex., 36.7-47.6 mm SL; all collected with holotype.

DIAGNOSIS. Distinguished from all other species of the genus by the combination of the following features: no maxillary tooth; two humeral spots, the first one black, well defined, longitudinally ovate, and with faint vertical expansions of dark pigment above and below; gray to black zigzag lines between longitudinal rows of scales; scales in lateral series 31-32; scales in predorsal series 10, irregularly distributed; and, anal fin rays 23-27.

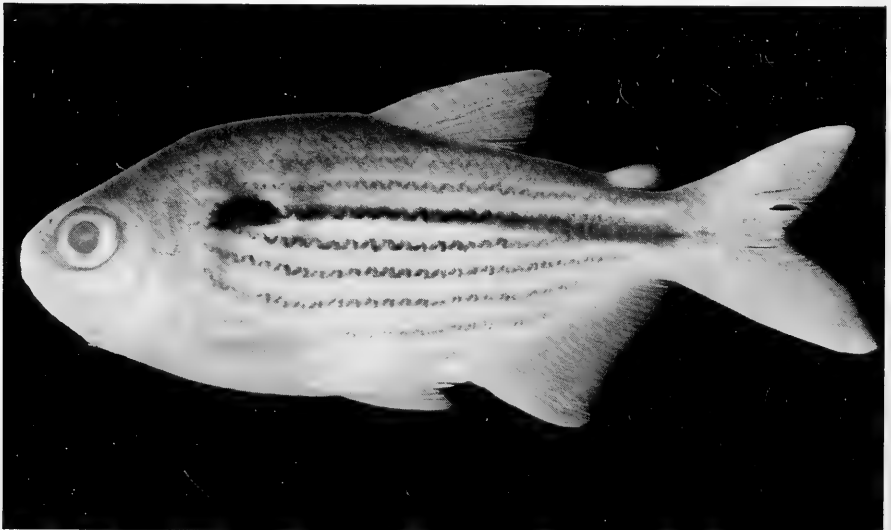


FIG. 1

Astyanax kullanderi, holotype, 57.2 mm SL, MNRJ 12427.

DESCRIPTION. Morphometric data are given in Table 1. Greatest depth at anterior dorsal fin origin. Dorsal head profile gently concave. Predorsal profile from nape to anterior dorsal fin origin slightly convex. Dorsal profile from dorsal fin origin to adipose fin origin, and from this point to dorsal procurent caudal fin rays concave. Ventral profile from the anterior tip of lower jaw to the base of last anal fin ray convex. Ventral caudal peduncle profile straight. Anal fin base slightly convex. Snout blunt, mouth terminal.

Origin of anal fin in a vertical through the base of last dorsal fin ray. Tip of pectoral fin reaching a vertical through the pelvic fin base. Tip of pelvic fin reaching between the urogenital papilla and the base of first anal fin ray. Distal margin of anal fin slightly concave. Caudal fin forked, dorsal and ventral lobes equal in size. Dorsal fin rays ii, 8, i; anal fin rays iii, 20-24; principal caudal fin rays i, 17, i; procurent caudal fin rays 11-13 + 10-11; pectoral fin rays i, 10-11, i; pelvic fin rays i, 7. Adipose fin present. Hooks on sides of last unbranched and first nine branched anal fin rays, and on first to fifth branched pelvic fin rays, all hooks curved and directed dorsally.

Scales in lateral series 31-32, all perforated; scales in transversal series 6 above lateral line, 5 below lateral line. Scales in predorsal series 10, distributed irregularly. Scale rows around caudal peduncle 16. Scales extending over about anterior 10% of caudal fin lobes.

Two teeth rows in premaxilla; outer row 4-5 teeth, gradually decreasing in length from the 1st to the last one, all tricuspidate, the median cusp longer; inner row 5 teeth, gradually decreasing in length from the 1st to the last one, 1st one longer than wide, other teeth approximately as long as wide, 1st tooth with 4 cusps, the 2nd cusp longer, 2nd and 3rd teeth with 5 cusps, the median cusp longer, and 4th and 5th teeth with 4 cusps, the 3rd cusp longer. No maxillary tooth. Dentary with one row of teeth; 4 anterior teeth gradually decreasing in length, 1st, 3rd and 4th teeth longer than wide, 2nd tooth as long as wide, 1st and 2nd with 6 cusps, the 2nd cusp longer, 3rd and 4th teeth with 4 cusps, the second cusp longer; 3-5 teeth posterior to and much smaller than 4 anterior ones, the 1st one tricuspidate or conical, other teeth conical. Branchiostegal rays 4. Gill-rakers 19-20. Infraorbital bones 6, the distal border of the 3rd one not reaching sensory tube of preopercle. Supraneurals 5. Vertebrae 16 + 19-20.

Colour in alcohol. Ground colour brown in dorsal region of body and head, becoming gradually yellow on sides. A black longitudinal stripe from humeral region to caudal fin base, becoming wider after posterior dorsal fin base, but no distinctive caudal spot. Brown to black zigzag longitudinal lines between longitudinal body rows of scales, darker in median region. A black, well defined, longitudinally ovate humeral spot, covering about 4 scales, with faint expansions above and below, and a second, more posterior, very faint and vertically elongate humeral spot. Small chromatophores over membranes of all fins. A few melanophores on median caudal fin region. Suborbital and opercular regions golden, with a few dark chromatophores.

ETYMOLOGY. Named after Sven O. Kullander, who collected the type series and made it available for study, as well as for his valuable contribution for neotropical Ichthyology.

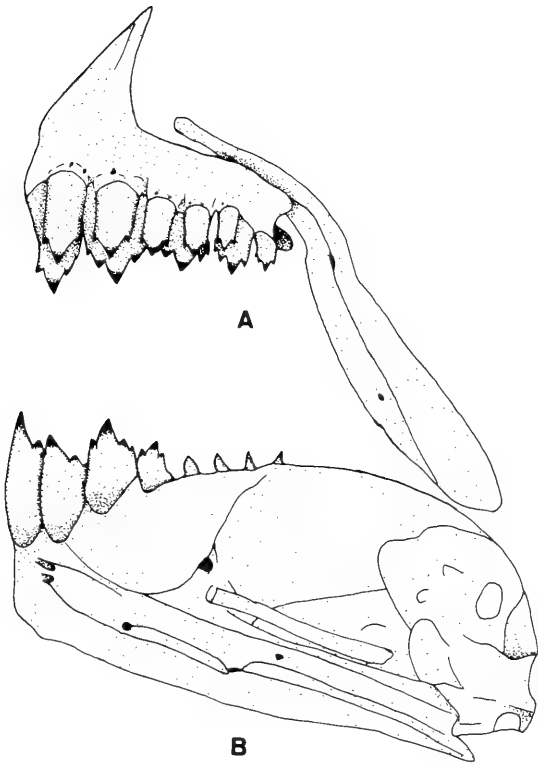


FIG. 2

Upper (A) and lower (B) left jaws of *Astyanax kullanderi* anterolateral view.

TABLE 1

Morphometric data of *Astyanax kullanderi*. Measurements 1-12 are expressed as % of standard length, 13-17 as % of head length. H: holotype.

	H		Paratypes						
Standard length (mm)	57.2	64.4	55.8	54.7	47.9	46.4	43.2	35.6	
1. Body depth	42.4	43.7	44.4	41.0	41.5	39.7	38.3	37.8	
2. Body width	16.0	17.2	18.7	15.6	15.4	14.1	14.4	14.2	
3. Predorsal length	55.2	56.8	57.1	54.5	54.9	55.2	52.7	53.3	
4. Prepelvic length	55.2	53.6	56.2	52.9	54.1	55.0	53.7	53.9	
5. Caudal peduncle depth	13.5	12.7	13.3	13.4	14.0	12.7	12.5	12.1	
6. Pectoral fin length	23.0	22.2	24.5	24.4	25.8	24.5	22.7	24.5	
7. Pelvic fin length	18.4	16.9	19.4	20.0	19.4	19.8	17.5	19.1	
8. Dorsal fin length	28.8	28.3	30.6	29.3	29.3	28.4	28.4	30.5	
9. Dorsal fin base length	14.9	14.1	14.5	14.7	15.4	13.8	12.7	13.9	
10. Anal fin base length	29.3	27.3	28.5	31.1	31.5	30.0	28.5	29.3	
11. Head depth	36.2	33.8	35.2	33.7	35.2	33.3	33.2	33.1	
12. Head length	27.4	26.5	27.9	27.5	28.6	28.4	28.9	29.4	
13. Head width	61.0	61.0	64.3	57.8	59.5	56.8	54.0	54.1	
14. Snout length	24.9	26.4	28.0	29.2	23.7	25.8	25.2	25.4	
15. Upper jaw length	43.8	44.0	43.1	42.5	39.8	42.4	43.6	42.1	
16. Eye diameter	35.1	33.1	36.7	36.5	38.7	42.0	38.4	37.8	
17. Interorbital width	35.8	39.0	35.7	36.5	36.5	33.3	35.2	34.9	

DISCUSSION

Species presently assigned to *Astyanax* have been grouped in the same genus by the common possession of: body completely scaled; few, if any tooth on maxilla; two series of premaxillary teeth, the inner row with 5 or more teeth; dentary with large, anteriorly positioned teeth, followed by other smaller teeth; series of lateral line pores complete; third infraorbital bone not in contact with sensory tube of preopercle; teeth not very compressed antero-posteriorly; caudal fin scaled only at its base; body not very elongate; maxilla not very long, upper jaw smaller than half of head length; and, scales not ctenoid (EIGENMANN 1917; GÉRY 1978). However, all these diagnostic characters are plesiomorphic or extremely labile in the Tetragonopterinae, and therefore do not indicate genus monophyly. In the same way, no monophyletic hypothesis for species groups within *Astyanax* is currently available.

Astyanax kullanderi presents a colour pattern of humeral spots consisting of a first ovate, well defined spot, with faint expansions of dark pigment above and below, and followed by a second, faint, vertical spot. Similar patterns are also present in some other *Astyanax* species such as *A. abramis* (Jenyns), *A. bimaculatus* (Linnaeus), *A. bourgeti* Eigenmann, *A. goyacensis* Eigenmann, *A. orthodus* Eigenmann, *A. poetzchkei* Ahl, *A. superbus* Myers, and *A. validus* Géry, Planquette & Le Bail, what may be an apomorphic condition, indicating close relationships. These species are currently placed in the subgenus *Poecilurichthys* Gill, by the common presence of scales irregularly distributed on predorsal series. Among those species, only *A. kullanderi*, *A. superbus*,

and *A. validus* have zigzag lines between longitudinal rows of scales, suggesting a close relationship. *Astyanax kullanderi* is distinguished from *A. superbus* by having fewer anal fin rays (23-27, vs. 29-33), fewer scales in lateral series (31-32, vs. 38-40), and no maxillary tooth (vs. 1-6). The new species further differs from *A. superbus* by the absence of caudal spot (vs. a caudal spot extending over median caudal fin rays), and a longitudinal black stripe on lateral midline (vs. no longitudinal stripe), and from *A. validus* by fewer gill-rakers on first arch (19-20 vs. 23).

Colour patterns comprising parallel longitudinal lines or spots rows on body sides also occur in other *Astyanax* species. *Astyanax bimaculatus* from the Paraguay and upper Madeira basins, *A. maximus* (Steindachner), and *A. saltor* Travassos have series of spots along the midline of each longitudinal row of scales, forming a pattern very distinct from *A. kullanderi* (lines between scale rows). *Astyanax lineatus* Perugia has a pattern of dark chromatophores around scales of body sides, chromatophores darker between the longitudinal rows of scales. This species does not present the diagnostic feature of the subgenus *Poecilurichthys*, not the colour pattern of humeral region above described, therefore considered a species not closely related to *A. kullanderi*.

ACKNOWLEDGEMENTS

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***Microstega homocolorum* sp. n. – the most frequently observed lachryphagous moth of man (Lepidoptera, Pyralidae: Pyraustinae)**

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***Microstega homocolorum* sp. n. – the most frequently observed lachryphagous moth of man (Lepidoptera, Pyralidae: Pyraustinae)** – The lachryphagous moths referred to as *Pionea aureolalis* (Lederer) in previous studies of lepidopterous lachryphagy are shown to consist of two species, *Microstega acutangulata* (Swinhoe) and *Microstega homocolorum* sp. n. So far, *M. homocolorum* is reported only from SW China and N Thailand where it is far more common than *M. acutangulata*, which is found from NW India to SW China and W Malaysia. 44 cases involving male adults of *M. homocolorum* and *M. acutangulata* (ratio about 8:1) drinking human tears have been witnessed but the main hosts are large ungulates and elephants. Observations in a zoo add Rhinocerotidae, Hippopotamidae, Giraffidae and Marsupialia as new host families/orders of lachryphagous Lepidoptera. *Pyralis ochrealis* Moore is synonymized with *Botys aureolalis* Lederer which is provisionally transferred to *Microstega*, as is *Paliga contractalis* Warren. Neither is lachryphagous but *M. aureolalis* takes mammalian body fluids other than lachrymation.

Key-words: Lepidoptera - Pyralidae - tear-drinking - mammalian hosts - Thailand.

INTRODUCTION

The lachryphagous moth *Microstega homocolorum* sp. n., referred to as *Pionea aureolalis* (Lederer, 1863) in several papers (e.g. BÜTTIKER, 1964; BÄNZIGER, 1973, 1983, 1992), is of potential medical and veterinary significance as discussed in the ecological section of this paper. Together with *Pyralis ochrealis* Moore, 1877, *Paliga contractalis* Warren, 1896 and *Pionea acutangulata* Swinhoe, 1901, it is one of four species which, due to their superficial similarity, have been synonymized as *Pionea aureolalis*. However, for some time I have had reservations about their conspecificity on behavioural and morphological grounds: *Pyralis ochrealis* and *Paliga contractalis*

apparently are not tear drinkers; the latter is clearly smaller and *M. homocolorum* consistently paler than the other species. Since the complex contains the moth which most frequently attacks human eyes, it is urgent to resolve the taxonomic identity of the species concerned.

Primary types of *ochrealis*, *contractalis* and *acutangulata* are in the Natural History Museum, London (BMNH), but efforts to locate the type of *aureolalis* proved unsuccessful in the four institutions where Lederer types are known to be kept. Through the courtesy of Mr M. Shaffer of the BMNH, who kindly checked MUNROE's (1958, 1970) lists of pyralid types in the BMNH and in the Zoological Institute, Academy of Sciences of Russia, St. Petersburg, it is evident that the *aureolalis* type is not in those two collections. My enquiries at the Museum für Naturkunde der Humboldt-Universität, Berlin and at the Naturhistorisches Museum Wien, were also negative. Rather than erect a neotype, Mr Shaffer suggested that this species is adequately defined by the type of *Pyralis ochrealis*, here considered to be a junior synonym of *aureolalis*, both with Sikkim as type locality. If a neotype for *aureolalis* were ever needed, it would have to be selected from a series of 4 specimens in the BMNH from Sikkim, which originate from the Lederer Collection and are probably conspecific with *ochrealis*. The moth found most often to trouble human eyes is not *aureolalis*, as previously assumed, nor is it any of the other named species, and it is here described as new.

There is a further species, *Pionea praepandalis* (Snellen), which superficially reminds *Pyralis ochrealis*, but it has not been synonymized with *Pionea aureolalis* and is not lachryphagous, hence it is not treated here. Its genitalia and feeding behaviour are closer to *Pyralis ochrealis* than to any of the other 4 species.

Genitalia studies of the relevant types (Mr M. Shaffer, pers. comm.) indicate that *ochrealis*, *contractalis* and *acutangulata* are different species, and that their generic classification will eventually have to be reassessed in a more comprehensive revision. They have traditionally been included in *Pionea* Guenée, 1845, which is a junior objective synonym of *Evergestis* Hübner, [1825], but the type species of *Pionea*, *Pionea margaritalis* Denis & Schiffermüller, 1775, is not congeneric with the species here discussed. For the present they are best included in the genus *Microstega* Meyrick, 1890 (type species *pandalis* Hübner, [1825]), which has been incorrectly synonymized with *Pionea*.

Type material is deposited in the Dept. Entomology, Fac. Agriculture, Chiang Mai University (DEFACU), the Natural History Museum, London (BMNH), the Muséum d'Histoire naturelle, Geneva, Switzerland (MHNG) and, when not specifically mentioned, provisionally kept in the author's collection for further study.

This is the eighth in a series of papers aiming to clarify the systematics of lachryphagous and other zoophilous Lepidoptera, the preceding having dealt with a notodontid (BÄNZIGER, 1989).

Microstega Meyrick, 1890

The generic placement of the following species in *Microstega* is, as mentioned above, provisional. While *M. acutangulata* and *M. homocolorum* sp. n. are evidently

congeneric, the other two species probably each belong to a different genus. A comprehensive revision of all related genera is needed to clarify their status.

***Microstega homocolorum* sp. n.**

Figs. 1, 2, 7-10, 15-18

Pionea aureolalis (auctorum nec Lederer): BÜTTIKER, 1964, *Verhandl. Naturf. Ges. Basel* 75: 233. BÜTTIKER, 1964, *World Health Organization WHO/EBL/29.64*: 7. BÜTTIKER, 1967 (1966), *Mitt. Schweiz. Ent. Ges.* 39: 156, 166, 174. BÄNZIGER & BÜTTIKER, 1969, *J. Med. Ent.* 6: 53, 56. BÄNZIGER, 1973 (1972), *Rev. suisse Zool.* 79: 1392, 1398, 1401, 1402, 1424, 1436-1438, 1449. BÄNZIGER, 1975, *Acta trop.* 32: 140. BÜTTIKER & NICOLET, 1975, *Rev. Elev. Méd. vét. Pays trop.* 28: 328. BÄNZIGER, 1983, *Mitt. Schweiz. Ent. Ges.* 56: 76, 79, 80, 82. BÄNZIGER, 1988, *Heteroc. Sumatr.* 2: 143. BÄNZIGER, 1988, *Nat. Hist. Bull. Siam Soc.* 36: 43. BÄNZIGER, 1989, *Mitt. Schweiz. Ent. Ges.* 62: 218. BÄNZIGER, 1990, *New Scientist*, 128, 1744: 51. BÄNZIGER, 1992, *Nat. Hist. Bull. Siam Soc.* 40: 92, 99, 101. PETERS, 1992, *Colour atlas of Arthropods in clinical medicine*: 266, Table 30, 269, Fig. 895.

Pionea aureolis (misspelling): BÄNZIGER, 1983, *Mitt. Schweiz. Ent. Ges.* 56: 73.

TYPE MATERIAL. Holotype ♂, *Thailand*: Chiang Mai Prov., Doi Suthep, Mae Nai, 1150 m, 3.xi.1988, Bänziger leg., genitalia slide 3027 (BMNH).

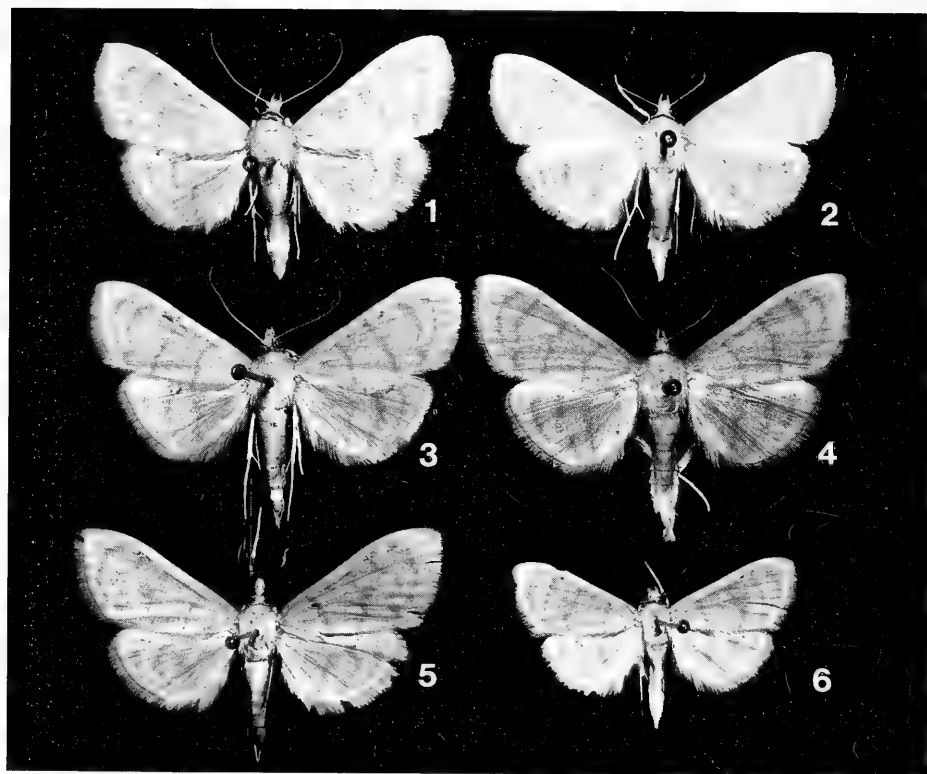
PARATYPES. 7 ♂, *ibid.* but 3.xii.1981 (DEFACU), 16.xi.1986, 6.xi.1987, 1., 3x14.viii.1988, genitalia slides 2361, 2638 (MHNG), 2804, 3026. 1 ♂, *ibid.* but Khun Chang Khian, 1340 m, 30.vii.1982. 1 ♂, *ibid.* but Sangwal, 1300 m, 20.ix.1986, genitalia slide 2303. 4 ♂, *ibid.* but Konthatharn Waterfall, 660 m, 4x5.xi.1987, genitalia slides 2631, 2632, 2633, 2634. 23 ♂, *ibid.* but area of Huay Kao, 330-370 m, 15.vii., 2x27.viii. (DEFACU), 2x1., 9., 2x12.xi.1972, 12. v., 3x19.v.1973, 2x6.xi. 1981, 12.xi.1990, 2x28., 31.x., 2x3., 5., 18.xi.1991, 18.vii.1992, genitalia slides 1001, 2227, 2228, 3008. 2 ♂, *ibid.* but Mae Taeng Distr., Huay Nam Dang, 1690 m, 2x5.viii.1986, genitalia slides 2234, 2246. 1 ♂, *ibid.* but Pong Düad, 650 m, 6.x.1982, genitalia slide 1458. 6 ♂, *ibid.* but Chiang Dao Distr., Kaeng Pan Tao area, 360-680 m, 26.x.1980, 10.vii.1982, 23.iv., 16.ix.1983 (BMNH), 24.ix.1983 (MHNG), 13.xi.1986, genitalia slides 1326, 1556, 2358. 1 ♂, *ibid.* but Ban Yang Pong, 500 m, 19.x.1990. 1 ♂, *ibid.* but road Chiang Dao-Phrao, 600 m, 15.xi.1989. 2 ♂, *ibid.* but Doi Chiang Dao, NW Pass, 1150 m, 24.v., 10.viii.1988, genitalia slide 2754. 4 ♂, Lamphoon Prov., Lii, 400 m, 4x20.viii.1980, genitalia slide 604, all Bänziger leg.

Other material [not included in paratype series]. SW China: 6 ♂, Yunnan Prov., Hsiao Meng Lun, 600 m, 3x15., 3x17.vi.1981, genitalia slides 934, 1181, 1182, all Bänziger leg.

DERIVATION OF NAME. The combination *homocolorum*, 'of human eyes', refers to the moth's habits of visiting the eyes of man.

DIAGNOSIS. Wingspan 23-27 mm. Overall colour pale yellow. Wing markings as shown in Figs. 1, 2. Medial line near the fore wing margin straight or convex. Male genitalia with tegumen distally rounded or slightly concave. Aedeagus with a patch of small cornuti near the distal end of the vesica.

DESCRIPTION. Male (Figs. 1, 2). Wingspan: 23-27 mm (one specimen among 52 measured is 28 mm), Ø = 25 mm. Head, thorax, abdomen, wings above pale yellow, paler on the underside, but head below the palps is pure white as are dorsally the fore and mid tarsi, and ventrally the mid tibiae. The fore tibia is dorsally white with a broad, dark yellow cross band in the middle. Filiform antennae are yellow. The proboscis, dorsally covered with white scales near the base, is 11 mm long, very thin. It has only minute sensillae on the distal section. Line markings of both wings upperside are faintly



FIGS 1-6

Species of *Microstega*. - 1-2. *M. homocolorum* sp. n. - 3-4. *M. acutangulata*. - 5. *M. aureolalis*. - 6. *M. contractalis*.

to clearly darker than the background. The arrangement of the basal, antemedial, medial and postmedial line are as shown in Figs. 1, 2. The medial line near the costa of the fore wing is straight or convex. A diffuse, occasionally very faint, dot is sometimes (5 out of 52 specimens) present near the costa between basal and antemedial line. Wings underside without markings.

Female. None caught (only males are lachryphagous).

Genitalia. Details as shown in Figs. 7-10. Distally the valve is relatively narrow, generally less than 1/2 to about 3/4 of the width of the aedeagus, and has a small projection on its ventral margin. The tegumen is rounded or slightly concave distally and lacks a finger-like projection proximally. The sclerotized, tooth-like structure of the sacculus, though rather variable, is relatively broad-based, short and only gently recurved. In some specimens it may have a tiny denticulation on its base. The ampulla tends to be rather massively club-like. Near the distal end of the aedeagus is a patch with spur-like sclerotizations and near the tip of the vesica is a patch with distinctive cornuti.

Immature stages. Unknown.

***Microstega acutangulata* (Swinhoe), comb. n.**

Figs. 3, 4, 11-14

Pionea acutangulata Swinhoe, 1901, Ann. Mag. nat. Hist. (7)8: 26.

TYPE MATERIAL EXAMINED. Holotype: Jaintia Hills 1901-178; *Pionea acutangulata* Swinhoe Type ♂, Pyralidae Brit. Mus. slide no. 8679 ♂. [BMNH].

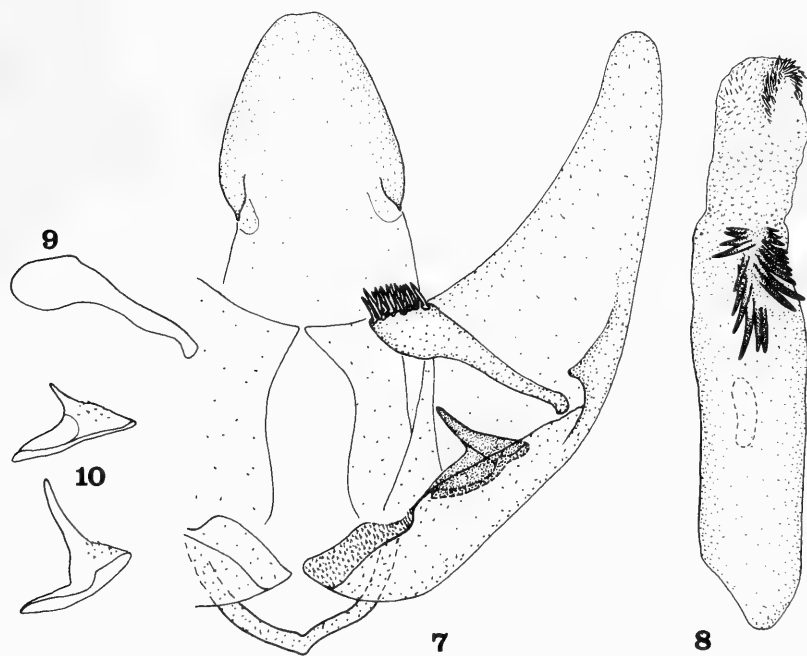
OTHER MATERIAL. *Thailand*: 1 ♂, Chiang Mai Prov., Doi Suthep, Huay Kao area, 350 m, 14.vii.1972. 4 ♂, *ibid.* but Doi Chiang Dao, NW Pass, 1150 m, 3x1.vi., 27.vii.1988, genitalia slide 2734, 2757, 2758, 2767. 1 ♂, *ibid.* but Ang Khang, 1400 m, 22.iv.1987, genitalia slide 2436. 4 ♂, Lamphoon Prov., Lii, 400 m, 4x20.viii.1980, genitalia slides 603, 605, 2229.

SW China: 1 ♂, Yunnan Prov., Hsiao Meng Lun, 600 m, 15.vi.1981, genitalia slide 933.

NW India: 7 ♂, Uttar Pradesh, Bhimtal, 1460 m, 24., 27., 29.vi., 2x16., 17., 18.vii.1987, genitalia slides 2500, 2525, 2555, 2556, 2559, 2595, 2597.

W Malaysia: 1 ♂, Kuala Lumpur, National Zoo, 3.vi.1971, genitalia slide 2231, all Bänziger leg.

DIAGNOSIS. As *M. homocolorum* but wingspan larger (26-31 mm, $\emptyset = 28$ mm, $n = 19$), overall somewhat darker yellow and with the line markings of the wings upperside more distinct. The medial line of the fore wing tends to be more removed from the antemedial and closer to the postmedial. The aedeagus lacks the patch of distinct cornuti near the tip of the vesica. The distal half of the valve is distinctly



FIGS 7-10

Male genitalia of *Microstega homocolorum* sp. n.; 8. aedeagus, dotted circle showing approximate position of cornuti in aedeagus with unextruded vesica; 9. variation of the ampulla; 10. variations of the tooth-like structure of the sacculus.

broad (generally only slightly narrower to wider than the aedeagus) and the projection on its ventral margin longer. The tegumen has distally a small bifid extension and proximally a finger-like projection (not always clearly visible). The sclerotized, tooth-like structure of the sacculus, though rather variable, is narrower based, longer and more recurved. The ampulla tends to be more slender.

***Microstega aureolalis* (Lederer), comb. n.**

Fig. 5

Botys aureolalis Lederer, 1863, Wien. ent. Monatschr. 7: 375, 473.

Pyrallis ochrealis Moore, 1877, Proc. zool. Soc. Lond. 1877: 614.

TYPE MATERIAL EXAMINED. Holotype of *B. aureolalis*: Sikkim, not found (possibly lost).

LECTOTYPE of *P. ochrealis*: Sikkim, Moore Coll. 94-106; *Pyrallis ochrealis* Moore (Type) ♀ [sic], Pyralidae Brit. Mus. slide no. 8678 ♂. [BMNH] lectotype hereby designated.

OTHER MATERIAL. *Thailand*: 1 ♂, Chiang Mai Prov., Doi Suthep, Chang Khian (site A), 1340 m, 27.x.1980, genitalia slide 2230. 1 ♂, *ibid.* but Nong Hoi, 1100 m, 25.x.1981, genitalia slide 990. 2 ♂, *ibid.* but Doi Chiang Dao, NW Pass, 1150 m, 15.x.1986, 16.xi.1987, genitalia slides 2650, 2763. 1 ♂, *ibid.* but Kae Noi, 1100 m, 12.vi.1982, genitalia slide 1293. 1 ♂, *ibid.* but Ang Khang, 1400 m, 21.v.1982, all Bänziger leg.

DIAGNOSIS. With 26-30 mm ($\emptyset = 27$ mm, $n = 6$) wingspan somewhat larger than *M. homocolorum*. Slightly darker yellow overall. Medial line near the costa concave (convex in *M. homocolorum* and *M. acutangulata*). Unlike in the other species treated here the nervature tends to be darker than the background, giving the wing the impression of a reticulation. In the genitalia the ampulla is very short and broad-based. The sacculus has several very long, sharply pointed, sclerotized projections. Distally the tegumen has two spur-like sclerotized projections, one curved outwardly the other curved inwardly. Aedeagus nearly twice as long, enlarged at both ends.

***Microstega contractalis* (Warren), comb. n.**

Fig. 6

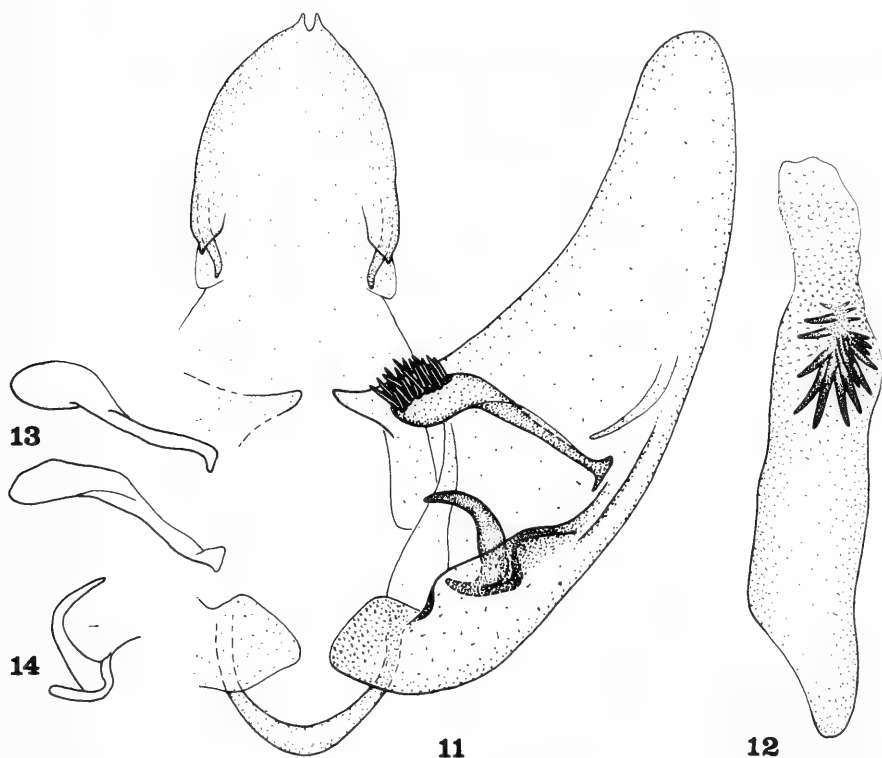
Paliga contractalis Warren, 1896, Ann. Mag. nat. Hist. (6)18: 123.

TYPE MATERIAL EXAMINED. Lectotype: Khasis, *Paliga contractalis* Warren Type ♂, Pyralidae Brit. Mus. slide no. 8677 ♂. [BMNH] lectotype hereby designated.

OTHER MATERIAL. *Thailand*: 2 ♂, Chiang Mai Prov., Doi Suthep, Khonthatharn Waterfall, 660 m, 9.xii.1985, 5.xi.1987, genitalia slide 2035. 2 ♂, *ibid.* but Mae Taeng Distr., Pong Düad, 650 m, 2x6.x.1982, genitalia slide 1428. 1 ♂, *ibid.* but Doi Chiang Dao, NW Pass, 1150 m, 17.vii.1986, genitalia slide 2218. 4 ♂, *ibid.* but Kae Noi, 1100 m, 4x12.vi.1981, genitalia slides 1294, 1295. 1 ♂, *ibid.* but Ang Khang, 1400 m, 7.xi.1991.

NW India: 3 ♂, Uttar Pradesh, Bhimtal, 1490 m, 21.vi., 18., 19.vii.1987, genitalia slide 2760, all Bänziger leg.

Diagnosis. With 18-22 mm ($\emptyset = 20$ mm, $n = 10$) wingspan clearly smaller than *M. homocolorum*. Also, the line markings of the wings tend to be less curved. The genitalia lack the sclerotized, tooth-like projection of the sacculus. Valve stouter, tegumen short and broad with two small but sharp extensions. Aedeagus without the patch of spur-like sclerotizations but patch of cornuti on vesica far more evident.



FIGS 11-14

Male genitalia of *M. acutangulata*; 12. aedeagus; 13. variations of the ampulla; 14. variation of the tooth-like structure of the sacculus.

ECOLOGICAL OBSERVATIONS ON *M. HOMOCULORUM*, WITH NOTES ON THE OTHER THREE SPECIES OF *MICROSTEGA*

DISTRIBUTION. — So far, *M. homoculorum* is reported from the upper north of N Thailand and the southernmost area of Yünnan, SW China, where it is sympatric with *M. acutangulata*. The two species are, in fact, syntopic at 4 sites. At two of them, Lii (Lamphoon Prov., Thailand) and Hsiao Meng Lun (Yünnan Prov., China) they were found on the same night, whereas at the other two sites, Doi Suthep and Doi Chiang Dao (Chiang Mai Prov., Thailand) they were caught on different nights. Syntopy is a further evidence that distinction of the two on a species, rather than subspecies, level is appropriate. *M. acutangulata*, which I also caught in W Malaysia and NW India (Uttar Pradesh), has a much wider distribution which encompasses completely that of *M. homoculorum*. However, *M. homoculorum* is far more common in N Thailand. The specimen seen sucking lachrymation on a water buffalo in N Laos (BÄNZIGER, 1983)

escaped and cannot be attributed to either of the two species, but *M. homocolorum* is the more likely in this area.

BIOTOPE. – *M. homocolorum* was found from 300 to 1700 m a.s.l. but was more common at the lower elevations. The forest types range from the dry Dipterocarp and mixed deciduous, to the hill evergreen. The moth was encountered more often in open, disturbed habitats than in the forest, though generally not very far from it. The other three *Microstega* species essentially fly in the same habitat although I have not yet caught *M. aureolalis* below 1000 m.

ANIMAL HOSTS. – Since earlier studies made no distinction between *M. homocolorum* and *M. acutangulata*, and because collections made during the oldest surveys, viz. in 1963 (BÜTTIKER, 1964) and 1965–1967 (BÄNZIGER, 1973), are not available to me, it is not known which species was found on which host. In my present collection (1971–1992), much larger than the older ones combined, are 55 *M. homocolorum* and 10 *M. acutangulata* from N Thailand. I take 6:1 as the nearest approximation of the true frequency ratio of the two species and also as the probability with which the oldest host records pertain to the two species. These host records are zebu (*Bos taurus indicus* L.), water buffalo (*Bubalus bubalis* (L.)), sambar deer (*Cervus unicolor* Kerr), pig (*Sus scrofa* L.), and Asian elephant (*Elephas maximus* L.) (BÜTTIKER, 1964; BÄNZIGER, 1973). The latter found male months that sucked mammalian body fluids including lachrymation also on banteng (*Bos javanicus* D'Alt.), goat (*Capra hircus* L.), and horse (*Equus caballus* L.). The new collections confirm zebu and horse as hosts of *M. acutangulata*, and also the water buffalo for *M. homocolorum*, but there is little doubt that all mentioned mammals can be hosts of both species.

During the most recent studies in the Chiang Mai Zoo (1990–1993) I have found *M. homocolorum*, among several other moth species, to imbibe tears from mammals which as yet were not known to be hosts of lachryphagous Lepidoptera: gayal (*Bos frontalis* (Lambert)), Burchell's zebra (*Equus burchelli* (Gray)), great one-horned rhinoceros (*Rhinoceros unicornis* L.), hippopotamus (*Hippopotamus amphibus* L.), giraffe (*Giraffa camelopardalis* (L.)), and western grey kangaroo (*Macropus fuliginosus* (Desmarest)) (Figs. 16–18).

The latter four are of particular interest as they belong to new host families (Rhinocerotidae, Hippopotamidae, Giraffidae) and the last one even to a new host order, the Marsupialia. With the three newly recorded families now all Old World ungulate families have representatives as hosts of lachryphagous Lepidoptera except the Tragulidae. These are unlikely hosts because of their diminutive size and high sensitivity.

The finding of the Marsupialia as a new host order is very unexpected because kangaroos had been investigated over a period of 10 months in the Zoo Negara, Kuala Lumpur, Malaysia, where no months were seen attacking the marsupials although ungulates in nearby cages were visited by tear drinkers. The new finding is not the result of a 'freak' event: during 30 investigations I witnessed 9 cases of *M. homocolorum* and 16 cases of other pyralids, noctuids and geometrids settling at the eyes of the kangaroos. Consequently my deduction (BÄNZIGER, 1988) that lachryphagy could not have evolved in Papua New Guinea and Australia due to lack of native hosts is



FIGS 15-16

Microstega homoculorum drinking tears from the eye of the author who photographed himself. Doi Suthep, 660 m, 5.xi.87; 16. *Microstega homoculorum* sucking lachrymation from the eye of a grazing western grey kangaroo. Huay Kaeo, 28.x.91.



FIGS 17-18

Microstega homoculorum imbibing lachrymation from the eye of a great one-horned rhinoceros. Huay Kaeo, 12.xi.90; 18. *Microstega homoculorum* at the eye of a very young hippopotamus. Huay Kaeo, 18.xi.91.

invalidated, and *Paliga damastesalis* Walker, which fed on ungulate and human eyes in Papua New Guinea, must not necessarily be a newcomer to those areas. It is almost certain that this, and possibly other species, will be confirmed to feed from large wild marsupials as well as introduced ungulates – domestic or feral – and probably man, also in Australia.

M. aureolalis and *M. contractalis* apparently are not lachryphagous; both were mostly caught at light traps but *M. aureolalis* was also observed sucking urine and skin-secretions (smeared off, not on the host).

MAN AS A HOST (Fig. 15). – While *M. homocolorum* is by no means the most common of over 100 species of Geometridae, Pyralidae, Notodontidae, Thyatiridae, Noctuidae and Sphingidae taking mammalian tears, it is remarkable as the most frequent among 23 species so far known to settle at human eyes (BÄNZIGER, 1992 and in prep.). *M. homocolorum* and *M. acutangulata* together sucked from the author's eyes on 40 instances, and on 4 more from the eyes of his colleagues or assistants. Based on the assumed frequency ratio of 6:1 this would roughly amount to about 38 successful attacks by *M. homocolorum* and 6 by *M. acutangulata*. Based on the actual specimens caught (which are fewer as quite a number of individuals escaped) the ratio is 8:1, which would amount to 39 and 5 cases respectively. These 39 feeding acts of *M. homocolorum* compare with 22 successful feedings by the pyralid *Filodes mirificalis* Lederer, 8 by the notodontid *Pydnella rosacea* Hampson, 6 each by geometrid *Hypochrosis flavifusata* (Moore) and pyralid *Paliga damastesalis* on human eyes.

FEEDING BEHAVIOUR. – Only male adults of the nocturnally active *M. homocolorum* (and *M. acutangulata*) are lachryphagous. Attacks on the author tended to occur erratically. Sometimes more than a year passed without a moth visiting his eyes, sometimes visits were sporadic at irregular intervals, and very occasionally many occurred during a single night. The activity of any moth probing one's eye is a rather unpleasant experience but compared to such aggressive tear drinkers as *Chaeopsestis ludovicae* Le Cerf (Thyatiridae) and *Tarsolepis elephantorum* Bänziger (Notodontidae), *M. homocolorum* is a very gentle visitor. The thyatirids and notodontids painfully claw the conjunctiva of both animals and man (BÄNZIGER, 1992) using their fore tarsi and at times even their middle tarsi. *M. homocolorum* is small, exhibits unobtrusive behaviour, has a thin, very flexible proboscis with only minute sensillae and is thus well adapted to suck fluids gently without causing damage or undue irritation to eye tissues. Tough hosts, such as large ungulates, rarely display any reaction to this moth. Thus the dangers of pathogen transmission would appear to be low. At the same time, however, *M. homocolorum* generally remains undetected by animals and continues feeding undisturbed for 5 minutes or more till satiation, since it causes little discomfort. Should *M. homocolorum* be proven to be a pathogen vector where mechanical damage is not necessary for transmission, the moth would have more time to transmit pathogens than the pain causing tear drinkers.

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eye during one of those glorious nights when lachryphagous moths display concerted attacks on man. Mr. Supot Methaphiwat, Director, Chiang Mai Zoo, gave permission for nocturnal investigations. Mr. W. Nässig, Frankfurt, assisted with nomenclature. Miss Saengdow Panthi helped typing the manuscript.

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Japygidés (Diplura) du Sud-Est asiatique n° 7: Malaysia (Sarawak), Indonésie (Java, Sumatra) et Sri Lanka – *Dicellurata Genavensia* XX –.

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Japygidae (Diplura) from South-East Asia n° 7: Malaysia (Sarawak), Indonesia (Java, Sumatra) and Sri Lanka – *Dicellurata Genavensia* XX –.

– This note is divided into 4 parts. 1) Topotypical specimens of *Indjapyx kraepelini* Silv. have been collected at Cibodas in Java. This enable the author to complete and amend SILVESTRI'S diagnosis (1930) and to describe the peculiar characteristics of the st.IIIA. – 2) Three new species are described from Sarawak and distributed between two new genera: a) *Pauperojapyx* n. gen. with two n. sp. for which two subgenera are created: *Pauperojapyx* s. str. n. subgen., type-species *P. (P.) iban* n. sp. and *Paucijapyx* n. subgen., type-species *P. (P.) kajan* n. sp.; b) the second n. gen., *Hutanjapyx* is monospecific, *H. simpan* n. gen., n. sp. – 3) The following new combination is proposed and discussed: *Indjapyx sumatranus* (Silv.) n. comb. = *Japyx sumatranus* Silvestri, 1916. – 4) A new specimen of *Deutojapyx greeni* (Silv.), endemic species of Sri Lanka, is recorded.

Key-words: Diplura Japygidae – Borneo – Sumatra – Java – Sri Lanka – Taxonomy – New genera and species.

INTRODUCTION

Les Japygidés au sens large ont, depuis la description par HALIDAY en 1864 de *Japyx solifugus*, toujours suscités un intérêt certain chez les entomologistes, mais très peu se sont spécialisés dans l'étude de ce groupe d'Insectes endogés, ayant tous le même aspect et dont les tailles s'échelonnent de 1,5 mm à près de 6 cm. De plus les captures de ces Arthropodes étaient le plus souvent dues au hasard, sans programme de recherche bien défini, sauf peut-être au début du siècle par deux grands entomo-

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logistes: K. v. Verhoeff et F. Silvestri dont la controverse au sujet des stades larvaires de ces Diploures est célèbre dans les annales de l'Entomologie.

Actuellement on dénombre 66 genres et entre 500 et 550 espèces. Malheureusement la plupart ne sont le plus souvent connues que par 1 ou 2 spécimens et plus d'une centaine placées dans le genre *Japyx* qui de ce fait est considéré comme cosmopolite, alors qu'il ne se rencontre que sur le pourtour du bassin méditerranéen.

Le seul travail rassemblant toutes les espèces décrites est le "Genera Insectorum: Diplura" de PACLT qui date de 1957; si ce travail est une précieuse source de documentation bibliographique, l'Auteur propose une classification des Japygidés parfaitement artificielle, réunissant sous un seul nom de genre préexistant jusqu'à 8 autres différents, sans tenir compte de leurs affinités réelles, il arrive même que des espèces placées dans ces "nouveaux genres" n'en possèdent pas tous les caractères retenus par PACLT; plus grave à mon avis, est le fait qu'un genre tel qu'il est défini par PACLT n'a, le plus souvent, qu'un lointain rapport avec la diagnose donnée par le premier auteur; par exemple *Burmjapyx* sensu Silvestri n'a que peu de chose à voir avec le *Burmjapyx* sensu Paclt qui réunit des espèces très disparates tant du point de vue morphologique que chorologique (cf. PAGÉS 1994). Je ne crois pas que l'utilisation de ce système soit un progrès dans la connaissance de la taxonomie des Japygidés; pour ma part je n'admets pas les synonymies génériques de PACLT et considère comme seules valables les diagnoses des auteurs précédents, Silvestri à quelques exceptions près.

A l'exception du "Japygidarum et Projapygidarum Catalogus", œuvre posthume de SILVESTRI (1949), malheureusement émaillée de nombreuses omissions et erreurs, il n'existe aucun autre travail d'ensemble que celui de PACLT; seules ont été publiées des mises au point de la faune japygidienne d'un pays donné, mais toutes sont antérieures au "Genera Insectorum" sauf celles concernant la France (PAGÉS 1979a) et la Grèce (PAGÉS 1979b) ainsi que les "Checklist" proposées par REDDELL (1983, 1985) qui sont des mises au point très complètes de nos connaissances sur les espèces de Japygidés s. l. des Amériques.

En ce qui concerne le Sud-Est asiatique toutes nos connaissances ne sont dues en dernière analyse qu'au hasard des récoltes, faites au gré des voyages d'entomologistes motivés ou de captures fortuites soumises à un spécialiste du groupe comme Silvestri ou Womersley par exemple. Quant à Bornéo et les îles indonésiennes nous ne connaissions que 9 espèces de Japygidés s. str. dont 7 *Indjapyx* et 2 "*Japyx*" avant que le Dr. B. Hauser, Conservateur et responsable du Département des Arthropodes et d'Entomologie I, au Muséum d'Histoire naturelle de Genève, ne mette en œuvre à partir de 1982, en collaboration avec le Dr. C. Lienhard, Chargé de recherches au même Département, un programme de récolte systématique des Microarthropodes du sol dans cette partie du monde et dans les régions avoisinantes.

En ce qui concerne les Diploures et plus particulièrement les Japygoidea, un très abondant matériel a été réuni. Il m'a été ainsi possible de décrire de l'Etat du Sabah (Nord Bornéo, Confédération de Malaysia) cinq espèces dont les 2 premiers Parajapygidés de ces régions et 3 espèces de Japygidés s. str. pour l'une desquelles j'ai dû créer un genre nouveau très particulier, *Kinabaluja**japyx* *disturbator* Pgs. (PAGÉS 1987 et 1994).

Dans cette note n° 7 sur les Japygidés du Sud-Est asiatique, j'étudie une partie des récoltes faites dans l'île de Java (Indonésie) et à Bornéo dans l'Etat du Sarawak (Confédération de Malaysia). Aux descriptions des deux nouveaux genres et des trois espèces inédites qu'il me semble nécessaire de créer, j'apporte de nouvelles données sur trois espèces déjà connues: *Indjapyx kraepelini* Silv. de Java, *Japyx sumatranus* Silv. de Sumatra et *Deutojapyx greeni* (Silv.) de Ceylan.

SILVESTRI (1930) a décrit *Indjapyx kraepelini* de "Tjibodas" (actuellement Cibodas) à Java; or la mission effectuée en 1987 a rapporté de cette station une dizaine d'exemplaires de cette espèce à tous les stades, dont des st. IIIA aux caractéristiques très inattendues; des compléments à la diagnose originale, en tenant compte de tous les stades rencontrés, feront l'objet de la première partie de cette note.

Je donne ensuite la description de trois espèces inédites du Sarawak, état qui fait suite vers le Sud à celui du Sabah. Je les répartis en deux nouveaux genres: *Pauperojapyx* n. gen. et *Hutanjapyx* n. gen.. Le premier qui forme, avec *Kinabalu-japyx* Pgs, un ensemble très particulier et isolé, est représenté par deux espèces, *iban* et *kajan*, pour lesquelles je crois nécessaire de définir deux sous-genres inédits: *Pauperojapyx* s. str., n. subgen. pour *iban* et *Paucijapyx* n. subgen. pour *kajan*. *Hutanjapyx* ne comporte que l'espèce *simpan* n. sp..

J'expose enfin les raisons qui me font placer *Japyx sumatranus* Silv. dans le genre *Indjapyx* Silv. et je signale un nouvel exemplaire de *Deutojapyx greeni* (Silv.), espèce endémique de Ceylan.

Tous les spécimens étudiés dans ce travail sont conservés dans les collections du Muséum d'Histoire naturelle de Genève.

Je tiens à remercier Mme M. Krähenbühl d'avoir dactylographié ce manuscrit et Mme E. Seraoui qui a reporté sur calque mes dessins originaux.

LISTE DES STATIONS

Etablie d'après la numérotation chronologique et la description des stations de la liste établie par le Dr. B. Hauser pour la mission de 1987 en Insulinde. Les spécimens ont été capturés soit directement à vue, soit après traitement des prélèvements par appareil Berlese (B).

Sar-87/14. – INDONÉSIE: Java: Cibodas: forêt de *Lithocarpus-Castanopsis* au-dessus du Jardin Botanique le long d'une gorge, prélèvement de sol dans les angles formés par les contreforts de deux arbres, 1380 m; 25.XI.1987, leg. B. Hauser (B)².

Sar-87/21. – INDONÉSIE: Java: Cibodas: forêt de *Lithocarpus-Castanopsis* au-dessus du Jardin Botanique, sentier touristique vers la cascade, prélèvement de sol dans les angles formés par les contreforts d'un grand arbre, env. 1380 m; 26.XI.1987, leg. B. Hauser (B)².

Sar-87/26. – INDONÉSIE: Java: Cibodas: Jardin Botanique, prélèvement de sol dans les angles formés par les contreforts de *Quercus pyriformis* Seeman près du ruisseau Cibodas, env. 1270 m; 27.XI.1987, leg. B. Hauser (B)².

² Extraction par appareil Berlese à Kuching (Sarawak).

Sar-87/60. — MALAYSIA: Sarawak: Serian: Penrissen Road 12 miles de Kuching, "Semongok Wildlife Rehabilitation Centre: Nursery Centre of the Forest Department", prélèvement de sol dans les angles formés par les contreforts de grands arbres, 50 m; 8.XII.1987, leg. B. Hauser (B)².

Sar-87/64. — MALAYSIA: Sarawak: route Kuching-Matang: mont Gunung Serapi, prélèvement de sol dans la forêt le long de la route vers la station TV, 670 m; 9.XII.1987, leg. B. Hauser (B)².

Sar-87/76. — MALAYSIA: Sarawak: Bako National Park: Jalan Lintang, prélèvement de sol dans les angles formés par les contreforts de *Austrobuxus nitidus* Miq. [= *Longetia malayana* (Benth.) P. & H.] (Euphorbiaceae), 30 m; 11.XII.1987, leg. B. Hauser (B)³.

Sar-87/80. — MALAYSIA: Sarawak: Bako National Park: Jalan Tanjong Sapi, prélèvement de sol dans les angles formés par les contreforts de grands arbres, 10 m; 11.XII.1987, leg. B. Hauser (B)³.

LISTE DES ESPÈCES TRAITÉES

Japygidae Haliday, 1864

Indjapyx kraepelini Silv., 1930

Stations: Sar-87/14; Sar-87/21; Sar-87/26.

Indjapyx sumatranus (Silv., 1916) n. comb.

Stations: Sumatra, Tandjong Slammat, dans un nid de *Labritermes buttelreepeni* Holmgr. (cf. SILVESTRI 1916).

Pauperojapyx (s. str.) *iban* n. gen., n. sp.

Stations: Sar-87/64; Sar-87/76; Sar-87/80.

Pauperojapyx (*Paucijapyx* n. subgen.) *kajan* n. sp.

Station: Sar-87/60.

Hutanjapyx simpan n. gen., n. sp.

Stations: Sar-87/60; Sar-87/80.

Deutojapyx greeni (Silv., 1930)

Station: n° 1 (cf. PAGÉS 1981).

1) COMPLÉMENTS À LA DIAGNOSE D'*Indjapyx kraepelini* Silv., 1930.

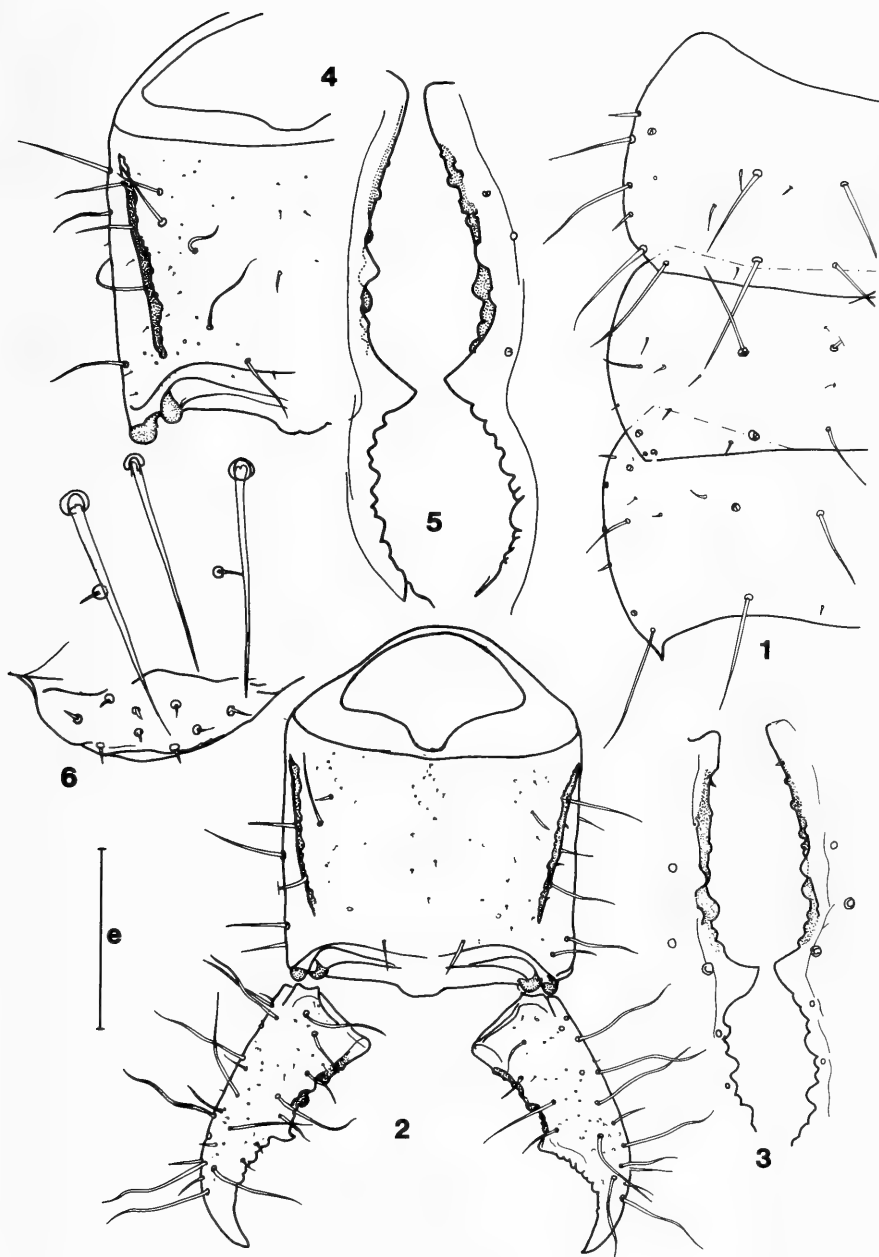
Matériel étudié: Sar-87/14 (1 st.IIIA de 4,77 mm); Sar-87/21 (1 sexe ? de 3,48 mm (resté très contracté), 1 ♀₁ de 5,4 mm, 1 ♀ ad. de 8,08 mm, 1 ♂ de 5,4 mm); Sar-87/26 (4 st.IIIA de 3,84 mm à 4,40 mm, 1 sexe ? de 4,2 mm, 1 ♀ ad. de 8,72 mm).

Soit 11 exemplaires: 2 sexes ?, 5 st.IIIA, 1 ♀₁, 2 ♀ ad. et 1 ♂.

Le traitement des spécimens à l'acide lactique ne permet pas toujours une extension parfaite, ni un éclaircissement suffisant pour déterminer sans ambiguïté le sexe, les papilles génitales restant souvent invaginées sous le sternite 8. Il est très vraisemblable d'admettre ici que les 2 individus de sexe indéterminé sont des st.IIIA.

² Extraction par appareil Berlese à Kuching (Sarawak).

³ Extraction par appareil Berlese à Genève.



FIGS 1-6

Indjapyx kraepelini Silv. 1. ♂ de 5,4 mm de Sar-87/21, tergites 5 à 7, e = 316 μ m. – 2. ♀ de 8,08 mm de Sar-87/21, tergite 10 et les cerques, e = 578 μ m. – 3. id., détail des marges internes des cerques, e = 312 μ m. – 4. ♀ ad. de 8,72 mm Sar-87/26, moitié gauche du tergite 10, e = 578 μ m. – 5. id., détail des marges internes des cerques, e = 294 μ m. – 6. ♀ de 8,08 mm de Sar-87/21 de 8,08 mm, organe glandulaire médian du premier urosternite, e = 63 μ m.

Cette espèce a été décrite par SILVESTRI (1930) d'après un ♂ apparemment adulte et une ♀ "juvenis".

La mission entomologique de 1987 a rapporté les 11 exemplaires détaillés ci-dessus qui, provenant tous de "Cibodas", sont donc topotypiques de ceux de SILVESTRI. Ce matériel me permet d'apporter quelques compléments et corrections à la diagnose originale et de faire connaître les caractères très remarquables des st. IIIA.

Nous envisagerons d'abord le cas des sexués.

TÊTE ET THORAX

Je n'ai rien de particulier à ajouter à la diagnose de SILVESTRI, sinon que mes exemplaires étant plus petits, à des stades plus précoces du développement post-embryonnaire, aucun ne présente d'aire pileuse céphalique.

ABDOMEN

Tergites : leur chétotaxie est conforme à ce que j'ai décrit comme typique chez les *Indjapyx*, c'est-à-dire avec les $ma = M^4$ à tous les tergites. Sur les tergites 3 à 7 de *kraepelini*, on notera donc 6+6M longs et surtout les détails suivants: 1) indifférenciation des *sma* qui disparaissent le plus souvent au tergite 7; 2) par contre, grand développement de m_2 , m_3 et mp qui sont presque aussi longs que les M ; 3) le faible nombre de soies très courtes chez nos exemplaires comme sur ceux de SILVESTRI.

Le tergite 8 est typique avec 4+4M longs dont 2+2 latéraux antérieurs (homologables aux M_2 et M_3) et 2+2 postérieurs (M_4 et M_5). Le 9e montre une rangée postérieure de minuscules soies espacées.

C'est à propos du tergite 10 que nos observations diffèrent apparemment le plus de la diagnose originale, même si l'on tient compte du fait que nos exemplaires sont, semble-t-il, à des stades plus jeunes. Comme chez le type, ce tergite est plus large d'un quart environ que long dans sa partie découverte et est légèrement plus étroit au niveau des condyles. En ce qui concerne les carènes, elles seraient chez le type "perparvis abbreviatis" alors qu'elles sont presque aussi longues que le scutum sur la Fig. XXXII et représentées de la même façon que celles d'*Indj. indicus* var. *borneensis*, qualifiées de "longis"; en fait elles occupent environ les 2/3 de la longueur du tergite et sont très colorées. La chétotaxie observée correspond assez bien avec celle du type; il y a 3+3M, dont 1+1 latéraux antérieurs, 1+1 latéraux intermédiaires et 1+1 intracarénaux subantérieurs; en outre, 1+1 soies intracarénales subpostérieures, 2+2 longues soies sur les carènes, 1+1 autres de même taille latérales postérieures, 1+1 submédianes postérieures longues ou assez courtes, 1+1 insérées au milieu des carènes et 2+2 latérales subantérieures et postérieures assez courtes ou courtes. Tous ces phanères n'ont pu être représentés sur nos figures 2 et 4.

⁴ On trouvera la liste des abréviations et des rapports utilisés dans PAGÉS (1954, 1984) et PAGÉS & SCHOWING (1958); v. ex. = valeurs extrêmes.

CERQUES

Aussi longs que la partie normalement découverte du tergite 10; environ 2 fois 1/4 aussi longs que larges à la base; aux deux cerques la largeur au niveau de la dent égale 0,80 fois celle à la base. Les cerques sont parfaitement symétriques, à dent pratiquement médiane, $r_d = r_g = 1,04$, triangulaire et équilatérale.

Marges prédentales : peu concaves avec aux deux cerques 3 tubercules supérieurs espacés et arrondis, dont le second est nettement plus développé que les autres; à droite on a 8 tubercules inférieurs arrondis dont le cinquième est plus fort que les autres; à gauche on note de même un tubercule, le quatrième ou le cinquième, plus important que les 5-6 autres.

Marges postdentales : fortement concaves avec 10-12 denticules arrondis dont les 4e et 7e à droite ainsi que le 3e ou 4e et 6e ou 7e au cerque gauche sont nettement plus saillants que les autres.

Cette description des marges pré- et postdentales correspond parfaitement avec la Fig. XXXII de SILVESTRI (1930).

Chétotaxie : typique, sans le *M* latéral antérieur.

Le st.IIIA de *I. kraepelini* présente plusieurs particularités intéressantes que je n'avais pas encore rencontrées de manière aussi nette.

TÊTE

Vertex : il montre une simplification notable de la chétotaxie par rapport à celle du st.IIIA d'*I. uvaianus* Pgs. prise comme type (PAGÉS 1984). Elle se rapproche de celle que j'ai décrite (PAGÉS 1978) chez la ♀ juv. d'*I. indicus* ssp. *modestior* Pgs. et chez *I. perturbator* Pgs., tous deux de Nouvelle-Calédonie.

Antennes et pièces buccales : typiques du genre; les antennes à chétotaxie beaucoup moins fournie que chez les adultes; *a* proximale, $p = 0,36$; aires pileuses sur les articles (20)-21-26-(27), peu fournies. La première lame du lobe interne des maxilles ne montre que 2-3 indentations, comme c'est la règle chez les st.IIIA ou B.

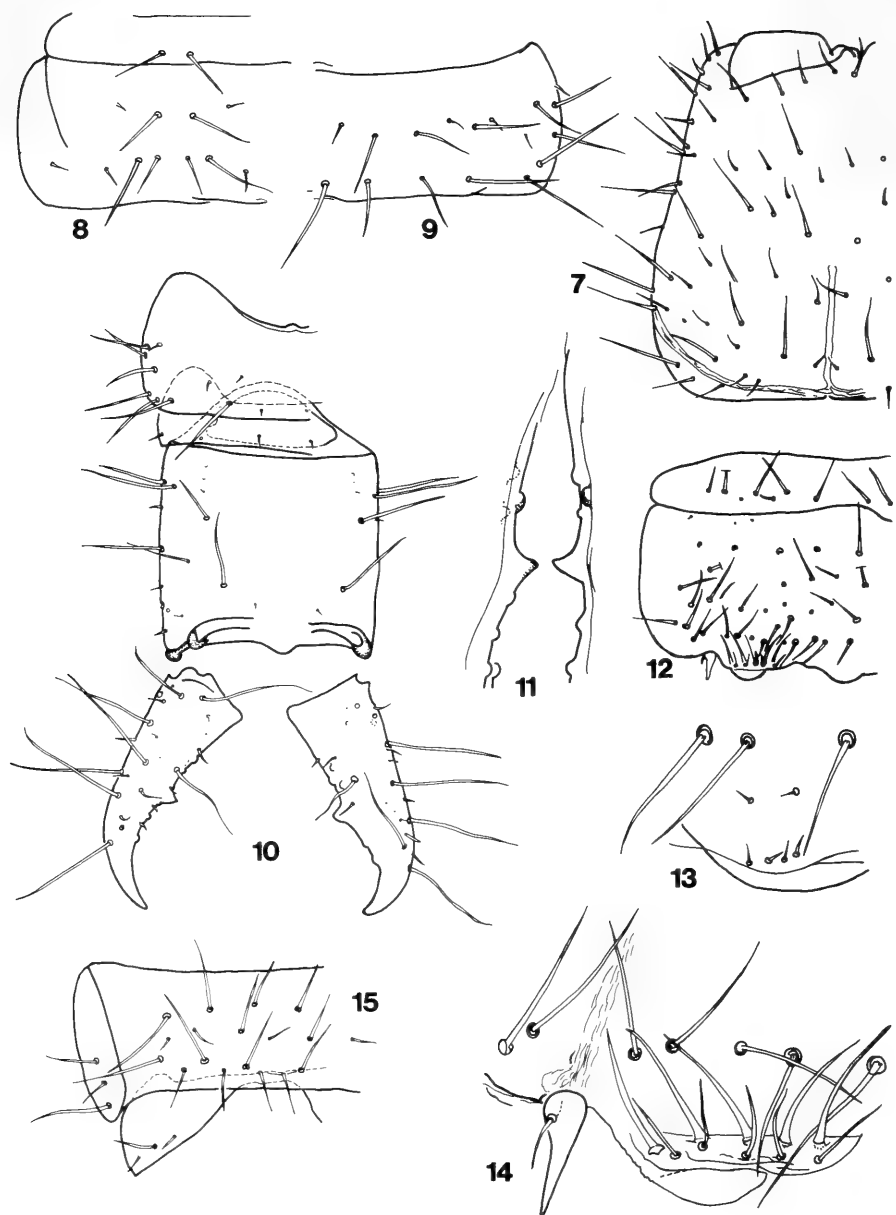
THORAX

Je n'ai rien noté de particulier; 5+5 *M* typiques sur chacun des notums et peu de soies. Pattes assez courtes, PIII atteignant à peine la limite préscutum-scutum du troisième urosternite.

ABDOMEN

Les tergites 1 à 9 ont la même chétotaxie que les adultes, en particulier les *ma* = *M* et le grand développement des *m*₂, *m*₃ et *mp*.

Le tergite 10 : il se distingue de celui des adultes par les caractéristiques suivantes: 1) il est pratiquement aussi large que long dans sa partie découverte; 2) les carènes sont nulles, mais 2 soies, antérieure et subpostérieure, sont insérées, de chaque côté, sur leur emplacement théorique.



Figs 7-15

Indjapyx kraepelini Silv. Toutes les figures se rapportent au st.IIIA de 4,72 mm de Sar-87/14. – 7. Vertex, e = 253 μ m. – 8. Tergite 1, e = 316 μ m. – 9. Tergite 4, e = 316 μ m. – 10. Tergites 8 à 10 et les cerques, e = 316 μ m. – 11. Marges internes des cerques, e = 158 μ m. – 12. Urosterite 1, e = 253 μ m. – 13. Organe glandulaire médian, e = 63 μ m. – 14. Organe subcoxal latéral droit, e = 63 μ m. – 15. Sternite et paratergite 8 et sternopleurite 9 droits, e = 253 μ m.

CERQUES

C'est à propos de ces appendices que les st.IIIA se distinguent le plus des sexués. S'ils sont aussi à peu près aussi longs que la partie normalement découverte du tergite 10, ils sont par contre 2,5 fois aussi longs que larges à la base; la largeur au niveau de la dent par rapport à celle à la base est assez différente d'un cerque à l'autre, à droite $ld/lc_q = 0,86$, à gauche ce même rapport égale 1,72; les deux cerques ne sont pas presque parfaitement symétriques comme chez les adultes; les dents bien que du type triangulaire à sommet dirigé vers la base du cerque ne se situent pas face à face, $r_d = 1,12$ et $r_g = 1,00$ en moyenne, la gauche étant toujours médiane.

Marges prédentales : subrectilignes avec chacune 2/1 tubercules arrondis de même taille; la présence de 2 tubercules supérieurs semble une caractéristique des stades jeunes de certaines espèces d'*Indjapyx*, comme par exemple chez la ♀₂ d'*I. indicus* ssp. *modestior* Pgs..

Marges postdentales : concaves avec seulement 2 denticules arrondis, largement espacés; un minuscule denticule arrondi supplémentaire peut se rencontrer, soit tout près de la dent, soit au contraire au-delà du denticule distal.

Chétotaxie : typique, sans le *M* latéral antérieur.

2) GENRES INÉDITS ET ESPÈCES NOUVELLES DU SARAWAK

Pauperojapyx n. gen.

Appartient à la famille des Japygidae.

Habitus et coloration typiques.

Le st. III est du type B.

Espèce-type: *Pauperojapyx iban* n. sp.

TÊTE

Sensiblement aussi large que longue, sa plus grande largeur est dans le quart postérieur. Antennes de 32 articles chez les espèces connues; 13 trichobothries en position normale, *a* médiane ou submédiane; 6 sensilles placoides en position typique sur l'article apical. Pièces buccales typiques de la famille, les 5 lames du lobe interne des maxilles pectinées.

THORAX

Chétotaxie : typique. Pattes normales assez allongées.

ABDOMEN

Les *ma* = *M* à tous les tergites. Tergite 10 légèrement trapézoïdal à petite base postérieure, sans carènes.

Urosternites : à chétotaxie typique. Soies à embase circulaire caractéristique différenciées ou non.

Organes subcoxaux latéraux: très petits, occupant moins du dixième de la largeur interstylière, à soies glandulaires d'un type particulier qui se retrouve chez *Kinabalujapyx* Pgs..

Organe glandulaire médian: à "pseudopori".

Styles et vésicules exsertiles: typiques aux urosternites 1 à 7.

Papille génitale ♂: de taille normale; l'orifice génital porte dans chacun de ses angles un bouquet d'une demi-douzaine de soies sans embase; appendices génitaux très développés, coniques, beaucoup plus longs que larges à la base. Le reste de la chétotaxie n'a pu être étudiée, les papilles étant restées invaginées sous l'urosternite 8.

Papille génitale ♀: typique, on note cependant chez nos exemplaires que la spermathèque est très longue et étroite.

Fossettes glandulaires: absentes chez les ♂.

CERQUES

Elancés, arqués et aigus. Dents nettement prémédianes, marges prédentales subrectilignes avec aux 2 cerques 1 ou 2 rangées de tubercules et une seule de denticules.

AFFINITÉS

Il apparaît qu'il existe dans l'ex-Bornéo du Nord un groupe de formes possédant un type de soies glandulaires très particulier aux organes subcoxaux latéraux: courtes, obtuses, déformables, plus "souples" que les soies glandulaires habituelles. Ce type ne m'était connu que chez *Kinabalujapyx* Pgs..

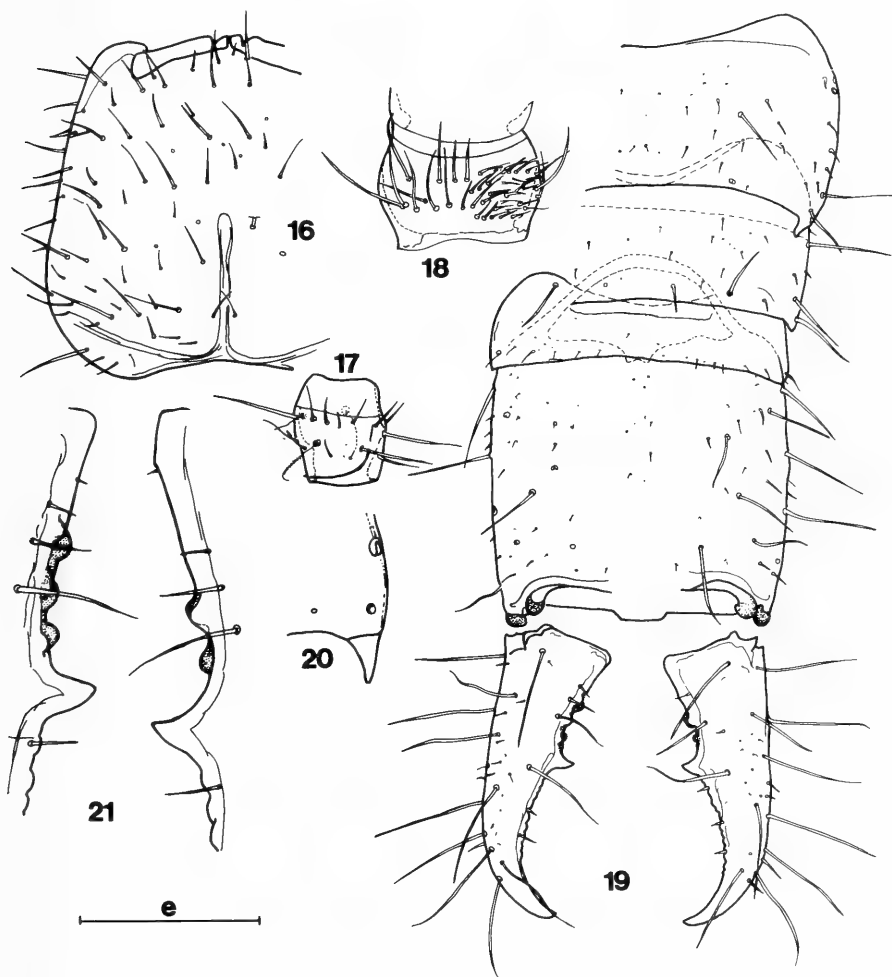
Si l'on tient compte aussi que ce dernier genre a le même nombre d'articles antennaires et que son premier stade à forceps est du type st.IIIB comme *Pauperojapyx*, je propose de les distinguer de la façon suivante: 1) Type *Kinabalujapyx* à soies glandulaires relativement nombreuses au niveau desquelles se trouve la vésicule exsertile de l'organe subcoxal latéral; la papille génitale ♂ a la partie médiane postérieure de sa base allongée et triangulaire; 2) Type *Pauperojapyx* à soies glandulaires très peu nombreuses formant un minuscule organe subcoxal situé médialement par rapport à la vésicule exsertile; on a donc le long du bord postérieur du sternite 1 la succession suivante: style-vésicule exsertile-organe subcoxal-organe glandulaire médian-organe subcoxal-vésicule exsertile-style; la partie postérieure de la base de la papille génitale ♂ est du type *Japyx*, hémisphérique.

En attendant l'étude d'un matériel encore plus abondant, je propose la systématique suivante. Deux genres, *Kinabalujapyx* et *Pauperojapyx*, caractérisés par la taille et la position relative de leurs organes subcoxaux, ainsi que par la forme de la partie postérieure de la papille génitale ♂.

Je subdivise *Pauperojapyx* en deux sous-genres caractérisés ainsi qu'il suit: 1) *Pauperojapyx* s. str. (espèce-type: *P. iban* n. sp.), à chétotaxie abdominale tergale typique, le sternite 1 présentant des soies à embase circulaire caractéristique en avant des organes subcoxaux latéraux et des cerques avec 2 rangées superposées de

tubercules; 2) *Paucijapyx* n. subgen. (espèce-type: *P. kajan* n. sp.) dont certains *sm* des tergites abdominaux sont différenciés en *M*, comme chez *Kinabaluja**japyx*, sans soies à embase circulaire caractéristique en avant des organes subcoxaux latéraux et des cerques armés chacun d'une seule rangée de tubercules.

Pour être complet, rappelons que *Kinabaluja**japyx* a une rangée de tubercules au cerque droit et 2 au gauche.



FIGS 16-21

Pauperojapyx (*P.*) *iban* n. sp. 16. ♂ holotype, vertex, $e = 957 \mu\text{m}$. – 17. id., 4e article antennaire gauche, $e = 316 \mu\text{m}$. – 18. id., 21e article antennaire droit, $e = 105 \mu\text{m}$. – 19. id., tergites 7 à 10 et les cerques, $e = 464 \mu\text{m}$. – 20. id., angle latéral droit du tergite 7, $e = 158 \mu\text{m}$. – 21. id., détail des marges internes des cerques, $e = 184 \mu\text{m}$.

En résumé, nous nous trouvons dans cette partie du Sud-Est asiatique devant un groupe de taxa bien distincts des autres Japygidés par les soies glandulaires des organes subcoxaux latéraux. Je pense que si mes observations sont confirmées par d'autres découvertes dans un matériel important, la création d'une sous-famille pourrait être raisonnablement envisagée.

DERIVATIONES NOMINORUM

- a) *Pauperojapyx*. De pauper, -eris: pauvre et, au sens figuré, peu abondant.
 b) *Paucijapyx*. De pauci, -ae: qui sont en petit nombre, quelques.

Dans les deux cas, allusion au nombre restreint de soies glandulaires des organes subcoxaux latéraux du premier urosternite.

Pauperojapyx (Pauperojapyx) iban n. sp.

Matériel étudié: Holotype: Sar-87/80, ♂ de 6,5 mm; paratypes: Sar-87/64 (1 ♀ de 5,12 mm); Sar-87/76 (3 st.IIIB de 2,62 mm, 3,19 mm et 3,23 mm, 1 ♀ de 4,31 mm); Sar-87/80 (1 ♀ de 5,12 mm).

TÊTE

V e r t e x : le schéma chétotaxique *Indjapyx* s'applique sans difficulté à cette espèce; on notera cependant l'absence des A2, ce qui est inhabituel, celles de V3 et la non-différenciation des L2 et L5.

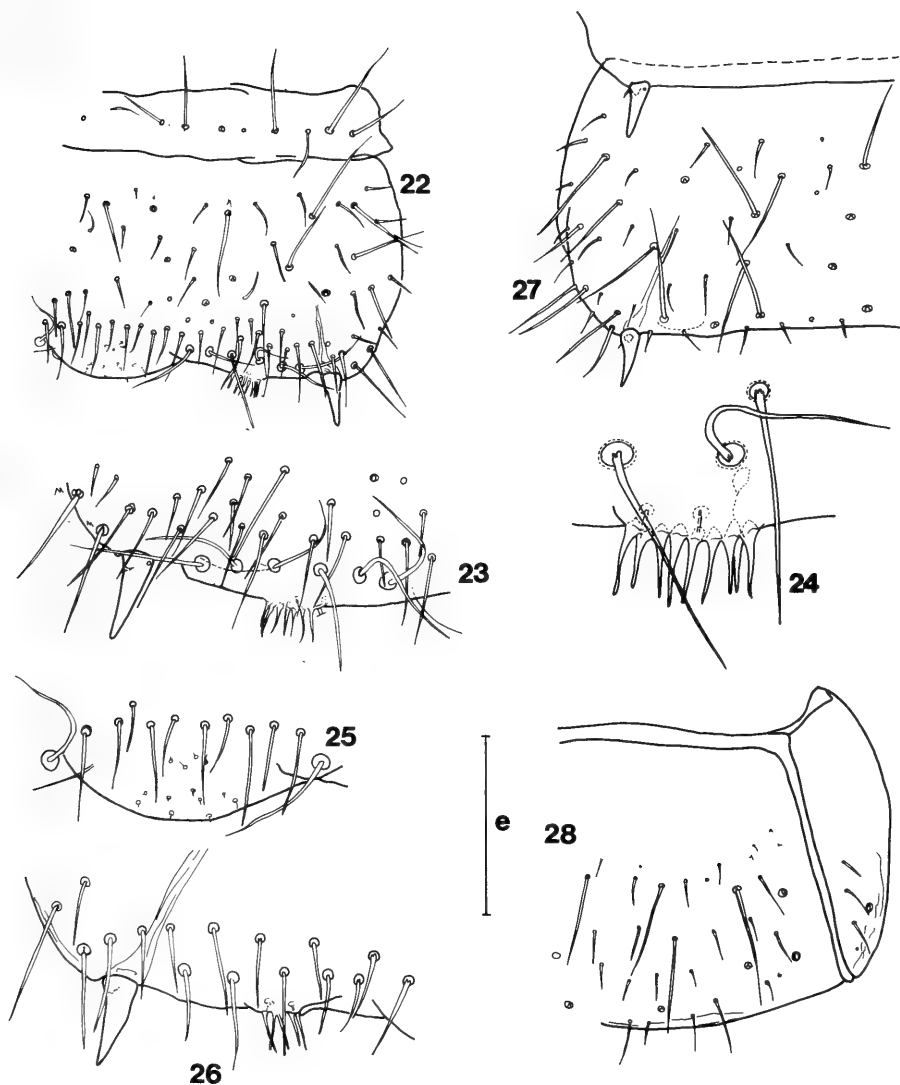
A n t e n n e s : de 32 articles avec 2 verticilles de soies raides, les proximales les plus longues, alternant plus ou moins régulièrement avec des sensilles sétiformes recourbées; 3 verticilles au pénultième article; aires pileuses très fournies sur les articles (15)-16-24-(25); les 13 trichobothries typiques, *a* légèrement distale, $p = 1,10$, la sensille sétiforme qui la remplace au st.IIIB est proximale, $p = 0,56$; 6 sensilles placoides en position typique sur l'article apical.

P i è c e s b u c c a l e s : typiques; les 5 lames du lobe interne des maxilles pectinées; palpes labiaux près de 2,4 fois aussi longs que larges à la base, les soies subapicales près de 2 fois aussi longues en moyenne que le palpe qui les porte.

THORAX

P r o n o t u m : les 5+5*M* typiques, longs, et 6-7 + 6-7 soies courtes; les *M*₁ sont légèrement plus longs que l'intervalle séparant leurs embases, $\epsilon = 1,12$.

M é s o - e t m é t a n o t u m : Préscutum: 1+1*M* longs, 1+1 soies assez courtes et 4-5 + 4-5 autres courtes ou très courtes et, au seul mésonotum, 1+1 soies à peine moins longues que les *M*. Scutum: les 5+5*M* typiques longs ou assez longs, les *M*₃ les plus longs, les *M*₂ du métanotum sont insérés nettement en arrière de la ligne joignant *M*₁ à *M*₃ et plus près de *M*₄ ou *M*₅ que normalement, environ 10+10 soies assez longues ou courtes.



FIGS 22-28

Pauperojapyx (P.) iban n. sp. 22. ♂ holotype, urosternite 1, $e = 253 \mu\text{m}$. – 23. id., organe subcoxal droit et soies à embase circulaire caractéristique, $e = 140 \mu\text{m}$. – 24. id., organe subcoxal latéral droit, $e = 63 \mu\text{m}$. – 25. id., organe glandulaire médian, $e = 140 \mu\text{m}$. – 26. ♀ de 5,12 mm de Sar-87/64, organe subcoxal latéral droit et le style, $e = 105 \mu\text{m}$. – 27. ♂ holotype, urosternite 3, $e = 253 \mu\text{m}$. – 28. id., sternite et paratergite 8 gauches, $e = 316 \mu\text{m}$.

P a t t e s : longues, les PIII atteignant presque l'urosternite 4; 4 à 6 soies spiniformes aux tarses; unguiculus réduit aux PI, bien net aux PIII où il mesure à peine le dixième de la longueur du tarse; la griffe postérieure plus de 1 fois $1/3$ aussi longue que l'antérieure et égale à peu près à la moitié du tarse correspondant.

ABDOMEN

T e r g i t e 1 : Préscutum: $1+1M$ longs et $1+2+1$ soies courtes. Scutum: $2+2M$ longs ($ma = M, M_5$), les sm non décelables, sauf les mp et les m_4 ; environ $8+8$ soies courtes disposées par paires inconstantes.

T e r g i t e 2 : $4+4M$ ($ma = M, M_1, M_{4-5}$) longs; quelques soies assez courtes ou courtes.

T e r g i t e s 3-7 : $6+6M$ ($ma = M, M_{1-5}$) longs ou assez longs; comme chez les *Indjapyx*, on notera la position très basse de $ma = M$, en arrière de la ligne joignant les M_1 ; m_3 assez longs, m_1 et m_2 très courts, les autres sm indiscernables; environ $15+15$ soies très courtes.

T e r g i t e 8 : près de 2 fois aussi large que long; $3+3M$ longs dont $1+1$ latéraux subantérieurs, $1+1$ sublatéraux subpostérieurs et $1+1$ submédians postérieurs; $1+1$ soies latérales postérieures longues, $1+1$ autres submédianes postérieures courtes et une vingtaine de soies très courtes réparties sans ordre apparent sur le tergite.

T e r g i t e 9 : 3,6 fois aussi large que long, sans M , mais avec une rangée postérieure d'une douzaine de soies très courtes, les $1+1$ les plus latérales 2 fois plus longues que les autres.

T e r g i t e 10 : à bords légèrement convexes, plus étroit au niveau des condyles postérieurs, 1 fois $1/5$ environ aussi long que large au niveau des M latéraux intermédiaires; carènes nulles; typiquement $6+6M$ longs ou très longs dont $2+2$ latéraux antérieurs et intermédiaires, $1+1$ sublatéraux subantérieurs, $3+3$ discaux, dont le subantérieur et le subpostérieur droit ou gauche peuvent n'être que des sm longs; $2+2$ soies latérales très longues ou longues et $1+1$ autres assez longues sublatérales subpostérieures; de nombreuses soies très courtes.

Angles latéraux postérieurs des tergites : nuls ou obtus aux tergites 1 à 6 et 9; en pointe allongée aiguë, recourbée vers la ligne médiane au tergite 7; en pointe courte et aiguë au 8e.

A c r o p y g e : bien net, trapézoïdal.

Longueurs relatives des segments 7 à 10 : 51-48-24-100.

S t e r n i t e 1 : Préscutum: $4+4M$ et $2-3+2-3$ soies assez longues ou courtes. Scutum: $14+14M$ dont les $13+13$ typiques et $1+1$ supplémentaires latéraux subpostérieurs insérés au-dessus des C_3 ; on notera que les B_3 sont situés en avant de la ligne joignant B_2 et B_4 ; de nombreuses soies assez courtes ou courtes dont une quarantaine forment une rangée assez régulière nettement en avant du bord postérieur du sternite; entre celui-ci et la rangée précédente, de chaque côté, entre le style et l'organe glandulaire médian, 6-7 soies longues, à large embase circulaire caractéristique. Chez les spécimens de Sar-87/76, il peut y avoir 2 de ces soies de chaque côté chez les st.IIIB ou aucune comme chez *P. (Paucijapyx) kajan* n. sp..

Organes subcoxaux latéraux : très peu développés; chez tous les individus ils sont situés médialement par rapport aux vésicules exsertiles, donc du côté de l'organe glandulaire médian; chez l'holotype, chacun occupe les 6/100 de la largeur interstylière et compte 8-9 soies glandulaires subégales, courtes, obtuses; chez les st.IIIB et les ♀, on n'observe que 1 à 2 de ces soies et 5 chez la ♀ de 5,12 mm; $SG/st_1 = 0,32$ (♂)- $0,44$ (♀)- $0,57$ (♀)- $0,72$ (st. IIIB). Le canal glandulaire égale à peu près la moitié de la longueur de la soie correspondante et se termine par un réservoir ovoïde assez important, sans goulot net. Soies sensorielles au nombre de 2 par organe quel que soit le stade ou le sexe; très courtes, $SG/SS = 3,4$ (st.IIIB) à $2,3$ (♂ holotype), $SS/st_1 = 0,2$ (st.IIIB) à $0,1$ (♂ holotype).

Organe glandulaire médian : très large, occupant près du tiers de la largeur interstylière, saillant, pourvu de 2 groupes de minuscules sensilles sétiformes chez les sexués, un antérieur de 3-4 en position médiane et 5-9, plus ou moins par paires, le long du bord postérieur de l'organe; chez les st.IIIB on n'observe que les 4 plus antérieures.

Sternites 2 à 7 : $16+16M$ longs, B_4 et les C de rang pair indifférenciés, assez longs ou courts; environ $20 + 20$ soies courtes ou très courtes; chez le ♂ on observe latéralement aux C_9 , $1+1$ longues soies.

Sternite 8 : $7+7M$ longs ou très longs disposés sur chaque demi-sternite sur 3 rangées de respectivement 2, 2 et $3M$ en partant de l'extérieur vers la ligne médiane.

Paratergites 8 : un M très long et 3 soies courtes.

Sternopleurites 9 : un M et 2-3 soies assez longues le long du bord postérieur.

Vésicules exsertiles : typiques aux urosternites 1 à 7; celles du 1er les plus développées.

Stylets : allongés, aigus, à cône secondaire net, à pore énigmatique nul ou obsolète; les st_1 sans soies; $st_1/st_7 = 0,76$, $s_7/st_7 = 0,24$.

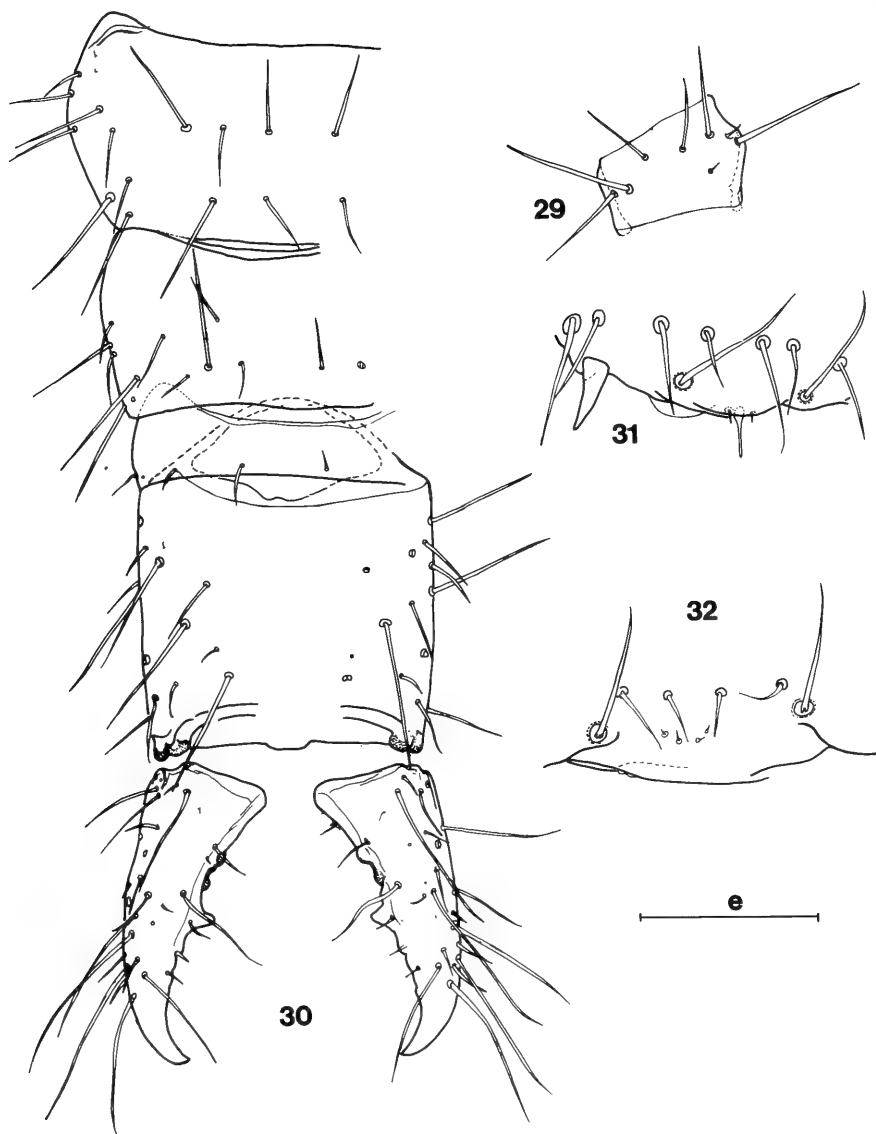
Papille génitale ♂ : typique du genre, appendices génitaux volumineux, coniques, 3 fois plus longs que larges à la base; dans chacun des angles latéraux de l'orifice génital une rangée de 5 soies sans embase, contiguës, arquées, assez courtes.

Papille génitale ♀ : typique de la famille; au plus 5 soies "glandulaires" de chaque côté; chez la ♀ de Sar-87/80 la spermathèque est étroite et très longue, atteignant le milieu du sternite 8.

Fossettes glandulaires : absentes chez les ♂.

CERQUES

Sensiblement aussi longs que la partie normalement découverte du tergite 10 (v. ex. = $1,00-1,11$); élancés, environ 2 fois $1/2$ aussi longs que larges à la base, $Lcq/lcq = 2,45$ (v. ex. = $2,32-2,59$), la plus petite valeur de ce rapport correspond à un st.IIIB; assez recourbé à leur extrémité qui est aiguë; en moyenne pour les 2 cerques, leur largeur au niveau de la dent égale des $4/5$ de leur largeur à la base, $ld/lcq = 0,80$ (v. ex. = $0,73-0,85$).



FIGS 29-32

Pauperojapyx (P.) iban n. sp. 29. st.IIIB de 3,23 mm de Sar-87/76, 4e article antennaire droit, e = 105 μ m. – 30. id., tergites 7 à 10 et les cerques, e = 158 μ m. – 31. id., organe subcoxal latéral et style droit, e = 63 μ m. – 32. id., organe glandulaire médian, e = 63 μ m.

Cerque droit : chez les adultes, la dent est prémédiane, $r_d = 0,69$, alors qu'elle est médiane au st.IIIB; très saillante, plus haute que large à la base, à sommet aigu dirigé vers la base du cerque, elle est pratiquement en triangle équilatéral au st.IIIB. Marge prédentale légèrement concave avec 1/2 tubercules arrondis, le supérieur situé au-dessus de l'inférieur proximal. Marge postdentale régulièrement concave, avec une quinzaine de denticules peu saillants, arrondis.

Cerque gauche : la dent, de même forme qu'au cerque droit, est prémédiane chez les adultes, $r_g = 0,76$, médiane chez les st.IIIB. Marge prédentale des adultes subrectiligne avec 2-3/3 tubercules arrondis. Marge postdentale comme au cerque droit.

Chez les st.IIIB, les 2 cerques sont parfaitement symétriques, à dents médianes, avec 1/2 tubercules et 3-5 denticules réduits à de simples ondulations des marges postdentales.

Chétotaxie : typique, sans le *M* latéral antérieur; très peu de soies très courtes ou extrêmement courtes.

AFFINITÉS

Ses antennes de 32 articles pourraient faire rapprocher *P. iban* de 2 autres espèces de Bornéo, *Indj. indicus* var. *bidicola* Silv. et "*Japyx*" *beccarii* Silv. du Mt Dulit, mais ses organes subcoxaux et ses cerques bien particuliers rendent toute confusion impossible.

DERIVATIO NOMINIS

Les Ibans ou, improprement, "Dayaks de la Mer" (Sea Dayaks) constituent la plus importante des ethnies proto-malaises venue de Sumatra et maintenant répandue dans toute l'île.

Pauperojapyx (Paucijapyx) kajan n. sp.

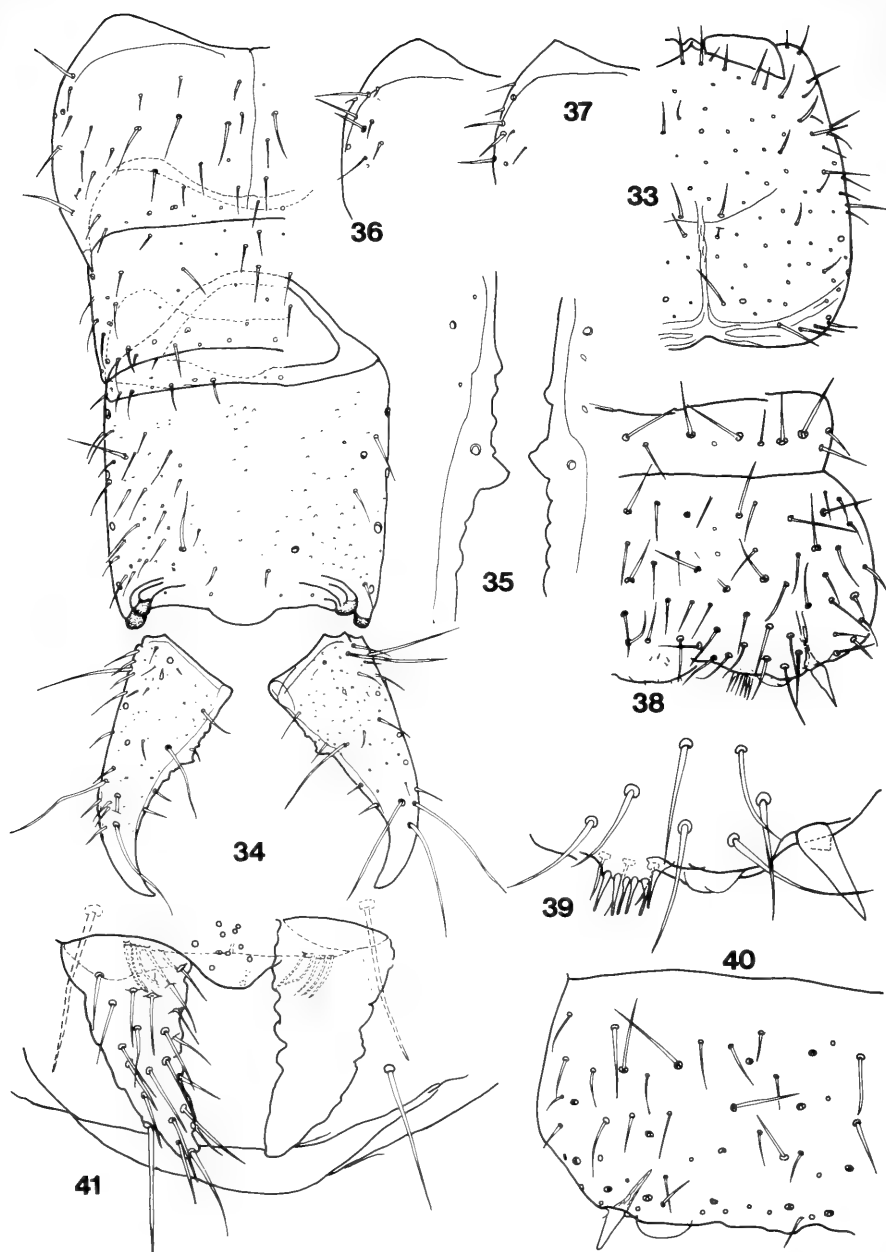
Matériel étudié : Holotype: Sar-87/60, ♂ de 4,5 mm; paratypes: de la même station (2 ♀ de 3,62 et 3,73 mm, 1 ♂ de 4,5 mm).

TÊTE

Vertex : la chute de la presque totalité des phanères ne permet pas de décrire convenablement la chétotaxie; on reconnaît cependant facilement la rangée des A avec les s1 et s2, les S4, S5, S6 et s5 et les P avec les s qui les accompagnent.

Antennes : de 32 articles à chétotaxie; aires pileuses sur les articles (16)-17-21-(22); les 13 trichobothries typiques, *a* médiane, *p* = 1,00; 6 sensilles placoides en position typique sur l'article apical.

Pièces buccales : typiques de la famille; les 5 lames du lobe interne des maxilles pectinées; palpes labiaux près de 2 fois aussi longs que larges à la base, les soies subapicales sont 1,75 fois aussi longues que le palpe qui les porte.



FIGS 33-41

Pauperojapyx (Paucijapyx) kajan n. sp. 33 ♂ holotype, vertex, $e = 253 \mu\text{m}$. – 34. id., tergites 7 à 10 et les cerques, $e = 229 \mu\text{m}$. – 35. id., détail des marges internes des cerques, $e = 70 \mu\text{m}$. – 36 et 37. id., détail de l'angle latéral antérieur des tergites 5 et 6, $e = 229 \mu\text{m}$. – 38. id., urosternite 1, $e = 158 \mu\text{m}$. – 39. id., organe subcoxal latéral et style gauches, $e = 63 \mu\text{m}$. – 40. id., urosternite 3, $e = 158 \mu\text{m}$. – 41. id., papille génitale, $e = 73 \mu\text{m}$.

THORAX

Pronotum : les 5+5*M* typiques, *M*₃ les plus longs, 10+10 soies assez longues à assez courtes.

Mésos- et métanotum : Préscutum: 1+1*M* longs et 1+1 soies très latérales longues. Scutum: les 5+5*M* typiques longs ou assez longs, les *M*₃ les plus longs de tous; une vingtaine de soies assez longues plus ou moins nettement disposées par paires.

Pattes : assez longues, les PIII atteignant le milieu de l'urosternite 3; 4+4 soies spiniformes aux tarses; unguiculus bien dégagé, la griffe postérieure près de 1,5 fois aussi longue que l'antérieure.

ABDOMEN

Tergite 1 : Préscutum: 1+1*M* longs; 1+1 ou 2+2 soies assez longues et 1-2+2 + 0-1 autres assez courtes ou courtes. Scutum: 2+2*M* longs (*ma* = *M*, *M*₅); *M*₁ = *sm* et *mp* assez longs, les autres *sm* assez courts; 3-4 + 3-4 soies courtes.

Tergite 2 : typiquement 4+4*M* (*ma* = *M*, *M*₁, *M*_{4.5}) assez longs; chez la ♀ de 3,62 mm, il n'y a que le *ma* = *M* droit; tous les *sm* sont assez courts ou courts comme une vingtaine de soies plus ou moins régulièrement disposées par paires.

Tergites 3 à 7 : 6+6*M* à 8+8*M*, *ma*, *m*₁ et *m*₂ différenciés en *M*, mais *m*₁ et *m*₂ tendent à redevenir des *sm* sur les derniers tergites. Ces *sm* = *M* sont relativement courts, de même taille que les *sm* typiques; environ 20 + 20 soies assez courtes ou courtes.

Tergite 8 : près de 1 fois 2/3 aussi large que long; 4+4*M* longs dont 1+1 latéraux subantérieurs, 1+1 sublatéraux subpostérieurs, 2+2 postérieurs latéraux et submédians; environ 20+20 soies assez longues à courtes et 3-4 médianes de mêmes tailles.

Tergite 9 : environ 3 fois 1/4 aussi large que long; sans *M*, mais avec une rangée postérieure d'une douzaine de soies courtes ou très courtes, les latérales pas plus développées que les autres.

Tergite 10 : légèrement trapézoïdal, 1 fois 1/4 aussi long que large au niveau des *M* latéraux intermédiaires; carènes nulles; 4+4*M* assez longs, dont 1+1 discaux postérieurs, 2+2 latéraux antérieurs et intermédiaires et 1+1 sublatéraux subantérieurs; 2+2 soies longues latérales subintermédiaires et postérieures; environ 20 soies assez courtes ou courtes sur chaque moitié du tergite et de très nombreuses soies très ou extrêmement courtes.

Angles latéraux postérieurs des tergites : nuls ou obtus aux tergites 1 à 6; en pointe aiguë bien différenciée au tergite 7; en pointe obtuse, peu marquée aux 8e et 9e.

Acropyge : large dessinant un arc de cercle assez régulier.

Longueurs relatives des segments 7 à 10 : 51-55-27-100.

Sternite 1 : Préscutum: 4+4*M* longs ou assez longs et 4+4 soies assez longues ou courtes; une soie médiale assez longue instable. Scutum: 11+11*M* longs ou assez longs, les *C*₁ et *C*₃ semblent absents et les *B*₄ sont indifférenciés et assez

longs; une trentaine de soies longues à courtes sur chaque demi-sternite; je n'ai pas observé de soies à embase circulaire caractéristique, on note seulement que les soies en arrière de la ligne soignant les C_3 ont une embase graduellement un peu plus grande que celle des autres phanères.

Organes subcoxaux latéraux : très particuliers. Chez le ♂, les soies glandulaires au nombre de 6 ou 7 sont courtes, obtuses, unisériées et occupent moins du dixième de la distance interstylière; chez les ♀₂ on en compte 1 ou 2 seulement, c'est-à-dire le même nombre que chez le st.IIIB de *Pauperojapyx* (s. str.) *iban*. Le canal glandulaire égale la moitié de la longueur de la soie glandulaire correspondante et se termine par un réservoir très petit, ovoïde, sans goulot décelable. Soies sensorielles au nombre de 3 chez le ♂, $SG/SS = 0,81$, et de 2 ou 3 chez les ♀₂, $SG/SS = 1,7-2,0$. $SG/st_1 = 0,35$ (♂) et $0,30-0,33$ (♀₂), $SS/st_1 = 0,43$ (♂) et $0,2$ (♀₂).

Organe glandulaire médian : peu différencié, peu saillant, large, occupant plus du quart de la largeur interstylière; 2+2 minuscules sensilles sétiformes à l'emplacement des 1+1 sensilles habituelles et 4 autres le long du bord postérieur de l'organe chez le ♂; chez les ♀, je n'ai observé que les 2+2 sensilles sétiformes.

Sternites 2 à 7 : 16+16*M* longs, B_4 longs, indifférenciés, comme les C de rang pair qui sont assez courts ou courts; environ 20+2-3+20 soies assez longues ou courtes.

Sternite 8 : 7+7*M* longs, disposés sur chaque demi-sternite sur 3 rangées de respectivement 2, 2 et 3*M* en partant de l'extérieur vers la ligne médiane.

Paratergites 8 : 1*M* long près de chacun des angles postérieurs.

Sternopleurites 9 : 1*M* long.

Vésicules exsertiles : typiques, relativement grandes aux uro-sternites 1 à 7.

Styles : allongés, aigus, à cône secondaire bien différencié; pore énigmatique indiscernable; les st_1 sans soies; $st_1/st_7 = 0,76$; $s_7/st_7 = 0,29$.

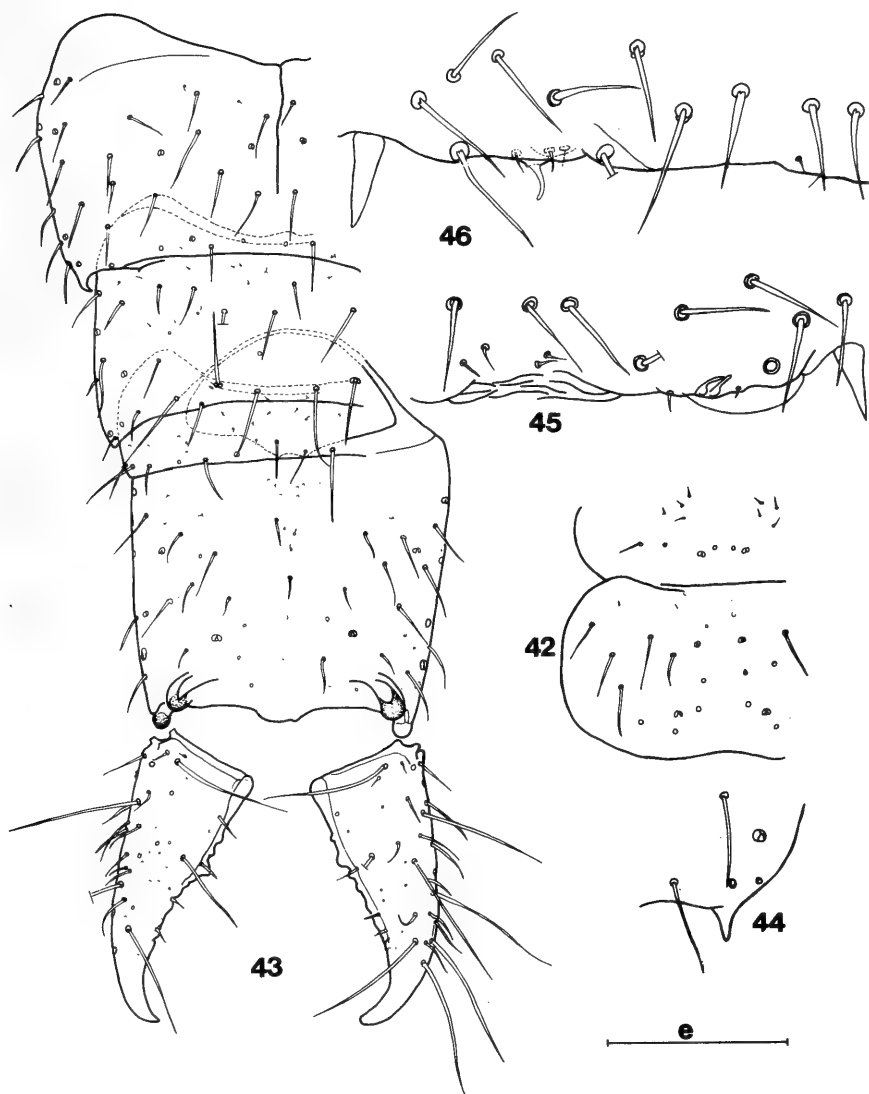
Papille génitale ♂ : typique; un bouquet de 5 soies sans embase à chacun des angles de l'orifice génital; appendices génitaux coniques, sensiblement 2 fois aussi longs que larges à la base.

Papille génitale ♀ : typique; 4 soies "glandulaires" de chaque côté de la base.

CERQUES

A peu près aussi longs que la partie normalement découverte du tergite 10, $Lcq/L10d = 0,97-0,98$, plus de 2 fois aussi longs que larges à la base, $Lcq/lc_q = 2,11-2,14$, peu arqués, la marge postdentale pratiquement dans le prolongement de la prédentale à droite, légèrement concave à gauche.

Cerque droit : dent triangulaire à sommet aigu chez le ♂, dirigé vers la base du cerque, prémédiane, $r_d = 0,56$ (♂)- $0,58$ (♀₂); la largeur au niveau de la dent égale 0,8 fois celle à la base (v. ex. = $0,77-0,81$); marge prédentale avec 1 tubercule arrondi; marge postdentale avec 0-2 denticules près de la dent, le reste de la marge rectiligne, plus ou moins nettement ondulé.



FIGS 42-46

Pauperojapyx (Paucijapyx) kajan n. sp. 42. ♀ de 3,62 mm de Sar-87/60, tergite 1, e = 158 µm. – id., tergites 7 à 10 et les cerques, e = 158 µm. – 44. id., angle latéral postérieur du tergite 7, e = 96 µm. – 45. id., moitié droite de la marge postérieure du sternite 1, e = 63 µm. – 46. ♀ de 3,73 mm de Sar-87/60, organe subcoxal latéral et style droits, e = 63 µm.

Cerque gauche : dent identique à celle de l'autre cerque, prémédiane, $r_g = 0,61-0,67$; la largeur au niveau de la dent égale 0,8 fois celle à la base comme au cerque droit; marge prédentale avec 2-3 tubercules assez arrondis, de tailles inégales; marge postdentale avec 2-3 denticules contigus et arrondis près de la dent, le reste de la marge irrégulier.

Chétotaxie : typique, sans le *M* latéral antérieur. Chez le ♂ on observe une multitude de minuscules sensilles (placoïdes?) dont 1 située sur le quart basal de chaque cerque est nettement plus grande.

AFFINITÉS

Incontestablement de la même lignée que *P. iban* elle s'en distingue facilement par les caractères propres au sous-genre *Paucijapyx* et immédiatement par l'allure et l'armature de ses cerques.

DERIVATIO NOMINIS

Les Kajans sont la tribu la plus importante des "Dayak de l'Intérieur"; ils se rencontrent dans le centre et l'est de l'île; vivant dans et de la forêt, leur survie est fortement compromise par la déforestation intensive qui existe dans tout le Sud-Est asiatique.

Hutanjapyx n. gen.

Appartient à la famille des Japygidae.

Habitus et coloration typiques.

Espèce-type : *Hutanjapyx simpan* n. sp.

TÊTE

Subcirculaire, à chétotaxie du vertex du type *Indjapyx*.

Antennes : de 34 articles chez l'espèce-type; quatrième article antennaire plus large que long, la trichobothrie *a* submédiane ou légèrement proximale; 8 sensilles placoïdes chez l'espèce-type.

Pièces buccales : typiques de la famille; 5 lames pectinées au lobe interne des maxilles.

THORAX

Chétotaxie : typique, 5+5*M*. Pattes assez courtes.

ABDOMEN

Chétotaxie tergale typique, la sternale avec *B*₅ et *C*₇ instables. Tergite 10 sans carènes. Angles du tergite 7 en pointe aiguë.

Organe subcoxaux latéraux et organe glandulaire médian : typiques du groupe *Indjapyx* et genres voisins.

Papilles génitales : apparemment typiques mais mal observées car restées invaginées sous le sternite 8 de nos exemplaires.

Fossettes glandulaires : nulles chez le ♂₁ (cf. PAGÉS 1967: p. 88).

CERQUES

Allongés, relativement étroits au niveau de la dent qui est du même type au 2 cerques: triangulaire équilatérale à sommet aigu dirigé vers la base du cerque. Dents postmédianes, la droite plus proximale que la gauche. Marges prédentales légèrement convexes, au moins basalement; une rangée de tubercules à droite, 1/n à gauche; marges postdentales concaves avec peu de denticules arrondis, à peine saillants.

AFFINITÉS

Voisin d'*Indjapyx* Silv., *Hutanjapyx* s'en écarte par ses antennes et ses cerques.

DERIVATIO NOMINIS

Hutan en malais signifie bois, forêt, biotopes où ont été récoltés les spécimens étudiés.

Hutanjapyx simpan n. sp.

Matériel étudié : Holotype: Sar-87/60, ♀ de 5,15 mm; paratype: Sar-87/80 (1 ♂₁ de 5,96 mm).

TÊTE

V e r t e x : chétotaxie du type *Indjapyx*, mais simplifiée; la série A est complète, mais sans les s; la S ne compte que 4 grands phanères (S1 et S3 absents); la M est complète; la I et la L sont très incomplètes; la P est complète, s comprises.

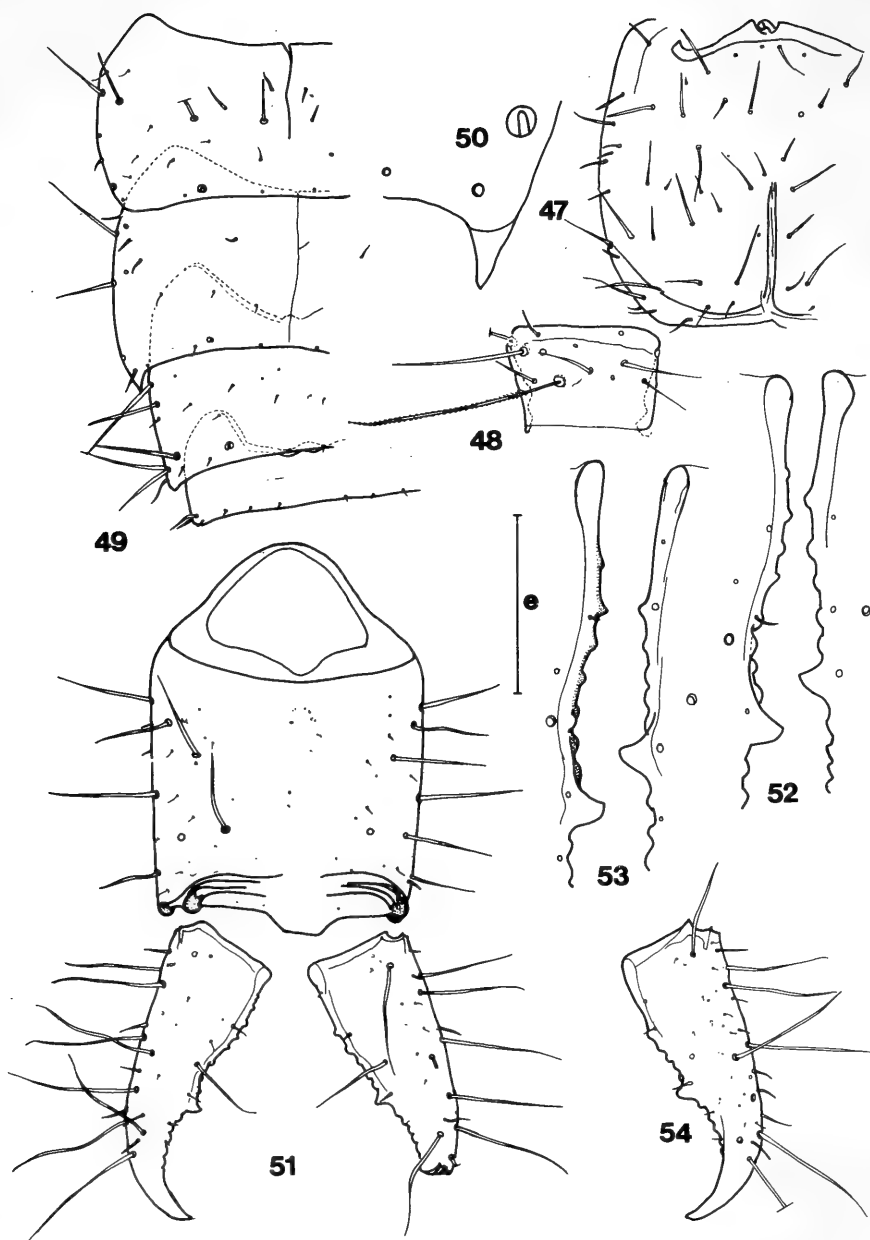
A n t e n n e s : de 34 articles à chétotaxie normale; on observe les sensilles recourbées à partir du 5e article; aires pileuses sur les articles 15 à 22; les 13 trichobothries typiques, *a* légèrement proximale, *p* = 0,75 en moyenne; 8 sensilles placoïdes sur l'article apical.

P i è c e s b u c c a l e s : typiques de la famille; les 5 lames du lobe interne des maxilles sont pectinées; palpes labiaux assez courts, environ 1,7 fois aussi longs que larges à la base, les soies subapicales, environ 2,2 fois aussi longues que le palpe qui les porte.

THORAX

P r o n o t u m : les 5+5*M* typiques, *M*₃ les plus longs, la longueur des *M*₁ égale 1,3 fois la distance séparent leurs embases; 3-4 + 3-4 soies courtes.

M é s o - e t m é t a n o t u m : Préscutum: 1+1*M* assez courts. Scutum: les 5+5*M* typiques, *M*₅ les plus longs; 3-6 + 3-6 soies assez courtes ou courtes.



FIGS 47-54

Hutanjapyx simpan n. gen., n. sp. 47. ♂₁ de 5,96 mm de Sar-87/80, vertes, e = 316 µm. - 48. / holotype, 4e article antennaire gauche, e = 158 µm. - 49. id., tergites 6 à 9, e = 276 µm. - 50. id., angle latéral postérieur droit du tergite 7, e = 60 µm. - 51. id., tergite 10 et les cerques, e = 276 µm. - 52. id., détail des marges internes des cerques, e = 122 µm. - 53. ♂₁ de 5,96 mm de Sar-87/80, détail des marges internes des cerques, e = 122 µm. - 54. id., cerque droit, e = 253 µm.

Pattes : assez courtes, les PIII atteignant à peine le présternite 3; 4+4 soies spiniformes, robustes et longues à tous les tarse; unguiculus et griffes bien développés, la postérieure égalant environ la moitié de la longueur du tarse, 1,3 fois celle de la griffe antérieure et près de 6 fois celle de l'unguiculus.

ABDOMEN

Tergite 1 : Présutum: 1+1*M* courts. Scutum: 2+2*M* (*ma* = *M*, *M*₅) longs; *msa*, *ma*, *m*₂ et *mp* assez longs à assez courts, les autres *sm* courts ou très courts.

Tergite 2 : 4+4*M*, *ma* = *M* assez longs, *M*₁, *M*₄ et *M*₅ longs.

Tergites 3 à 7 : 6+6*M* à 5+5*M*, les *ma* nettement différenciés en *M* assez longs au tergite 3 peuvent être soit nuls, soit de très courtes soies, soit des *sm* des 2 côtés ou d'un seul côté des tergites.

Tergite 8 : 1,7 fois aussi large que long; 5+5*M* longs dont 4+4 homologues aux *M*₂, *M*₃, *M*₄ et *M*₅ et 1+1 postérieurs sublatéraux entre *M*₄ et *M*₅; 1+1 soies longues entre les *M*₄ et les *M* supplémentaires (*m*₃?); environ une trentaine de soies très courtes dont les 1+1 latérales antérieures (= *m*₁?) et les 1+1 latérales postérieures nettement plus longues.

Tergite 9 : près de 2 fois 2/3 aussi large que long; pas de *M*, mais une rangée postérieure de minuscules soies et 1+1 autres courtes latérales postérieures.

Tergite 10 : entre 1,4 et 1,5 fois aussi long que large, à bords subparallèles, sans carènes; 4+4*M* longs dont 2+2 discaux, subantérieurs et subpostérieurs, ces derniers ayant tendance à se modifier en *sm*, et 2+2 latéraux antérieurs et intermédiaires; 3+3 soies longues ou assez longues dont 2+2 antérieures et subpostérieures sur l'emplacement théorique des carènes et 1+1 latérales postérieures; soies courtes ou très courtes peu nombreuses.

Angles latéraux postérieurs des tergites : nuls aux tergites 1 à 5; obtus, mousses aux 6e, 8e et 9e; en pointe aiguë, bien différenciée du reste au tergite 7.

Acropyge : typique à bords arrondis.

Longueurs relatives des tergites 7 à 10 : 46-47-27-100.

Sternite 1 : Présutum: 4-5+4-5*M* longs et 3-4+3-4 soies assez courtes à très courtes. Scutum: 11+11*M*, les *B*₅ simples soies assez longues, les *C*₁ nuls, les *C*₃ difficiles à distinguer des soies qui les entourent; à noter que *A*₄ n'a pas été représenté sur la figure 55; une quarantaine de soies à embase circulaire caractéristique forment une rangée assez régulière en avant des organes subcoxaux et médian; quelques autres, peu nombreuses entre cette rangée et une ligne passant par les *C*₂, *B*₄ et *C*₃.

Organes subcoxaux latéraux : ils occupent environ le quart de la largeur interstylière, peu saillants. Chez le ♂₁ 6 et 7 soies glandulaires, 8 chez la ♀, de taille sensiblement égale à celle du *st*₁ (v. ex. = 0,89-1,06); 16 soies sensorielles chez le ♂₁ et 17-18 chez la ♀, *SS/st*₁ = 0,51 en moyenne (v. ex. = 0,47-0,53); *SG/SS* = 1,95 (v. ex. = 1,90-2,27).

Organe glandulaire médian: large saillant; 8 à 10 minuscules sensilles sétiformes ("pseudopori"?) dont 2 nettement en avant de la ligne théorique d'articulation de l'opercule, les autres formant deux groupes symétriques sur l'opercule.

Sternites 2 à 7: typiquement 15+15*M*, mais *B*₅ et *C*₇ présents ou non, différenciés en *M* ou non; les *B*₄ et les *C* de rangs pairs sont, comme à l'accoutumée, indifférenciés ou nuls.

Sternite 8: 7+7*M* longs disposés sur chaque demi-sternite sur 3 rangées longitudinales de 2, 2 et 3*M* en partant de l'extérieur vers la ligne médiane.

Paratergites 8: 1*M* long, intermédiaire; environ 10+10 soies courtes ou très courtes; 1+1 soies subpostérieures assez longues et 2-3 soies courtes.

Sternopleurites 9: 1*M* long et 2-3 soies courtes ou très courtes.

Vésicules exsertiles: typiques aux urites 1 à 7.

Styles: allongés, aigus à pore énigmatique et cône secondaire nets; en moyenne $s_1/st_1 = 0,26$, $st_1/st_7 = 0,89$, $s_1/s_7 = 1,00$, $s_1/st_7 = 0,23$.

Papille génitale ♂: typique du ♂₁ (cf. PAGÉS 1967).

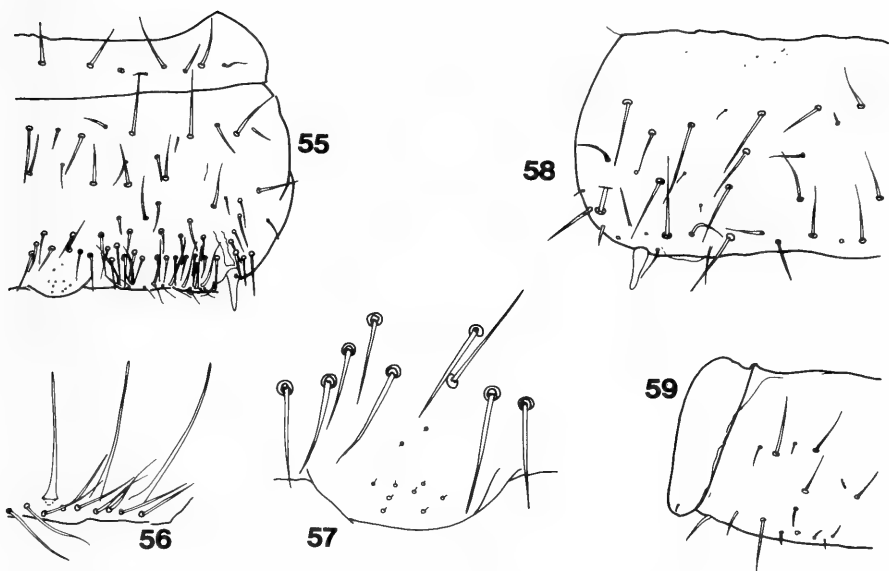
Papille génitale ♀: restée invaginée sous l'urosternite 8 je n'ai pu l'étudier convenablement; compte tenu de la taille de l'exemplaire, du développement des organes subcoxaux latéraux et de la pilosité générale, il pourrait s'agir d'une ♀ déjà "âgée", mais, si l'on observe sans difficulté une spermathèque très fine et très longue (elle atteint le milieu du sternite 8) et 2 lobes antérieurs et 1 postérieur, on ne détecte aucun phanère; on devrait donc conclure qu'il s'agit d'une ♀₁ encore plus simple que celles que j'ai décrites en 1967; on peut aussi envisager le cas d'une régression temporaire (ou saisonnière).

CERQUES

A peu près aussi longs que la partie normalement découverte du tergite 10, élancés, $Lcq/lcq = 2,53$ en moyenne, peu arqués à l'extrémité qui est aiguë, la largeur au niveau de la dent est égale environ aux 3/4 de celle à la base, $ld/lcq = 0,75$ (v. ex. = 0,71-0,79), c'est le cerque droit qui est le plus large à ce niveau, $ld/lcq = 0,78$, le gauche le plus étroit, $ld/lcq = 0,73$; les dents, postmédianes, sont triangulaires équilatérales, à sommet aigu dirigé vers la base des cerques.

Cerque droit: à dent nettement plus proximale qu'au cerque gauche, $r_d = 1,20$; marge prédentale subrectiligne, légèrement convexe avec 5 tubercules unisériés, arrondis, peu saillants, le proximal distant des suivants; marge postdentale concave avec 5-6 denticules arrondis peu marqués, sauf les 2 premiers.

Cerque gauche: à dent distale, $r_g = 1,59$ (♂₁)-1,44 (♀); marge prédentale légèrement convexe sur sa moitié basale, concave ensuite vers la dent; 1/7 tubercules peu saillants, arrondis, sauf le second proximal du ♂₁ et les second et quatrième proximaux de la ♀ qui sont aigus, le supérieur situé au-dessus de l'intervalle séparant les 5e et 6e inférieurs; marge postdentale concave avec 5-6 denticules arrondis peu marqués, sauf les deux près de la dent.



FIGS 55-59

Hutanjapyx simpan n. gen., n. sp. 55. ♀ holotype, urosternite 1, e = 211 μ m. – 56. id., détail de l'organe subcoxal gauche, e = 63 μ m. – 57. id., organe glandulaire médian, e = 63 μ m. – 58. id., urosternite 3, e = 211 μ m. – 59. id., sternite et paratergite 8 droits, e = 316 μ m.

Chétotaxie : typique, le *M* latéral antérieur indifférencié; quelques rares soies très courtes vers les marges extérieures.

DERIVATIO NOMINIS

L'holotype a été récolté dans une réserve forestière, en malais "Hutan Simpan" d'où le nom du taxon.

3) POSITION GÉNÉRIQUE DU *Japyx sumatranus* SILV., 1916.

En 1916 SILVESTRI décrit un *Japyx sumatranus* n. sp. d'après un spécimen récolté dans un nid de *Labritermes buttelreeperi* Holmgr. à Tandjong Slammat dans l'île de Sumatra.

Par la position très proximale de la trichobothrie *a* du quatrième article antennaire, la forme des angles postérieurs du tergite 7 et la chétotaxie de ses organes subcoxaux latéraux, ce taxon appartient indubitablement au genre *Indjapyx* Silv.: *Indjapyx sumatranus* (Silv., 1916) n. comb. (= *Japyx sumatranus* Silv., 1916). Cela est confirmé indirectement par la présence d'une aire de soies très courtes sur la partie postérieure du vertex et par l'apparente symétrie des deux cerques.

Les organes subcoxaux latéraux sont voisins de ceux d'*Indj. annandalei* Silv. et la pauvreté de leur chétotaxie me paraît indiquer un stade assez juvénile, ce qui semble être corroboré par la très petite taille de l'exemplaire, 3 mm, et par l'absence de carènes sur le tergite 10. Le fait que SILVESTRI ne mentionne qu'une seule rangée de 3-4 tubercules assez petits ("sat parvis") proximale à la dent sans indiquer s'il en existe ou non une rangée supérieure n'est pas, à mon avis, un obstacle à l'appartenance de cette espèce au genre *Indjapyx*, le ou les tubercule(s) supérieur(s) pouvant être très peu différencié(s) et, en 1916, ce caractère n'avait pas toute l'importance qu'il a pris par la suite.

A mon avis *Indjapyx sumatranus* (Silv.) présente des caractères intermédiaires à ceux d'*I. annandalei* Silv. et *I. seymouri* Silv..

4) *Deutojapyx greeni* (SILV.) DE CEYLAN

Un exemplaire de cette espèce endémique de Ceylan a été reconnu au cours des ultimes contrôles des divers tamisages provenant de la campagne entomologique effectuée dans cette île en 1970 par MM. Besuchet et Löbl. Il s'agit d'un ♂ adulte récolté le 29.01.70 à la limite supérieure de la forêt, juste au-dessous du sommet du Pidurutalagala (ca. 2500 m); il s'ajoute aux 8 exemplaires déjà connus de cette station et porte à 17 le nombre de spécimens que j'ai pu étudier (PAGÉS 1981).

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A revision of the species of the subfamily Habrocerinae (Coleoptera: Staphylinidae) of the world.

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A revision of the species of the subfamily Habrocerinae (Coleoptera: Staphylinidae) of the world. – At present the subfamily Habrocerinae comprises two genera, *Habrocerus* Erichson and *Nomimocerus* Coiffait & Saiz. A worldwide revision of the genus *Habrocerus* Erichson yielded altogether 13 valid species. 7 new species are described: *H. ibericus* sp. n. from Southwest Europe, *H. simulans* sp. n. from the Eastern Mediterranean region, *H. cyprensis* sp. n. from Cyprus, *H. canariensis* sp. n. from the Canary Islands, *H. indicus* sp. n. from India, *H. costaricensis* sp. n. from Costa Rica and *H. schillhammeri* sp. n. from Sumatra. *H. capillaricornis* ssp. *pisidicus* Korge is raised to species rank. Lectotypes are designated for *Habrocerus capillaricornis* (Gravenhorst) and *H. schwarzi* Horn. *Nomimocerus tichomirovae* Filatova is transferred to *Habrocerus*. *H. magnus* Leconte from North America is excluded from the genus. 3 new species of *Nomimocerus* Coiffait & Saiz, formerly known to contain only the type species, *N. marginicollis* (Solier), are described: *N. longispinosus* sp. n., *N. peckorum* sp. n., both from Chile, and *N. parvispinosus* sp. n. from Argentina and Chile. The systematic position and the morphological characteristics, particularly the structure of the male abdomen, of *Habrocerus* and *Nomimocerus* are outlined. For each species details and illustrations of differential characters as well as data on distribution and, if available, bionomics are presented. Diagnostic keys allowing separation of *Habrocerus* and *Nomimocerus* adults are provided.

Key-words: Coleoptera - Staphylinidae - Habrocerinae - *Habrocerus* - *Nomimocerus* - World - Taxonomy - new species

THE SUBFAMILY HABROCERINAE: INTRODUCTION AND SYSTEMATICS

The genus *Habrocerus* was fixed by ERICHSON (1839) by monotypy. Its type species, *H. capillaricornis*, had been described as *Tachyporus capillaricornis* by GRAVENHORST in 1806. In the 19th century, *Habrocerus* was largely considered to belong to the subfamily Tachyporinae, apparently because of its general similarity in

body shape with some tachyporine genera, until GANGLBAUER (1895) established the subfamily Habrocerinae. BERNHAUER & SCHUBERT (1916) placed four genera in the Habrocerinae: *Amblyopinus* Solsky, *Edrabius* Fauvel, *Eumitocerus* Casey and *Habrocerus* Erichson, which at that time contained four species. *Amblyopinus* and *Edrabius* were later excluded from the subfamily and placed in the Amblyopininae (SEEVERS 1944). *Eumitocerus* proved to be a synonym of *Trichophya* Mannerheim (BLACKWELDER 1952; MOORE & LEGNER 1975). Consequently, *Habrocerus* was the only genus left in the Habrocerinae until COIFFAIT & SAIZ (1965) established the genus *Nomimocerus*, whose type species had been described by SOLIER (1849) as *Tachyporus marginicollis* and treated by subsequent authors as *Habrocerus marginicollis* (Solier).

Together with some other subfamilies COIFFAIT (1972) excluded the Habrocerinae from the Staphylinidae and elevated the subfamily to family rank, the Habroceridae containing two genera, *Habrocerus* and *Nomimocerus*. However, hardly any of the 20th century authors working on the higher classification of Staphylinoidea have shared his view concerning the Habrocerinae; they maintained (and so do we) the status of subfamily, although they may have disagreed considerably with regard to other aspects of the general systematics of Staphylinidae (see LAWRENCE & NEWTON 1982; NAOMI 1985). It should be added that CROWSON (1967), in contrast, places the Habrocerini (containing *Habrocerus* and *Olisthaerus* Dejean [!]) in the Tachyporinae, together with Trichophyini, Tachyporini, Bolitobiini and Hypocyptini. According to a recent study by ASHE & NEWTON (1993) the Habrocerinae are the sister group to the Trichophyinae.

The Habrocerinae differ from other Staphylinidae (a) in that the hind coxae form triangular plates (Fig. 1f), (b) in that only five abdominal segments are visible in the males, (c) in that the sclerotization of the lobes and the bulbus of the aedeagus is reduced and (d) especially in the remarkably modified urites VIII and IX in the males (COIFFAIT 1972; COIFFAIT & SAIZ 1965; CROWSON 1967). Since all of these characters can be considered apomorphic, there remains little doubt that the Habrocerinae represent a monophyletic taxon.

As can be concluded from zoogeographic evidence the Habrocerinae appear to be rather old phylogenetically: (1) The subfamily is widely distributed in both the northern and the southern hemisphere, including the Palaearctic, the Oriental, the Nearctic and the Neotropical region. (2) The range of the *Habrocerus schwarzi* group shows a disjunct pattern with species occurring in the New World as well as the East Palaearctic and the Indo-Malayan subregion. (3) The subfamily contains species with an apparently relict distribution. (4) The genus *Nomimocerus* is restricted to the temperate zones of South America.

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Csch	Private collection, Mr M. Schülke, Berlin
Czan	Private collection, Dr. A. Zanetti, Verona
BMNH	British Museum of Natural History (Dr. P.M. Hammond)
BRI	Biosystematics Research Institute, Ottawa (Dr. J.M. Campbell, Dr. A. Smetana)
DEI	Deutsches Entomologisches Institut, Eberswalde (Dr. L. Zerche)
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IRSNB	Institut Royal des Sciences Naturelles de Belgique (Mr I. Brogniez, Dr. K. Desender)
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MCSNV	Museo Civico di Storia Naturale di Verona (Mr R. Pace)
MCZ	Museum of Comparative Zoology, Cambridge Mass. (Mr S.P. Cover)
MHB	Museum für Naturkunde der Humboldt-Universität, Berlin (Dr. M. Uhlig)
MHNG	Muséum d'Histoire naturelle, Genève (Dr. I. Löbl)
MNS	Museum für Naturkunde, Stuttgart (Dr. W. Schawaller)
NHMW	Naturhistorisches Museum Wien, Vienna (Mr H. Schillhammer)
ZIAWP	Zoological Institute of the Academy of Sciences St. Petersburg (Dr. G.S. Medvedev)

The authors' collections will be abbreviated as follows: Cass (coll. Assing) and Cwun (coll. Wunderle).

THE GENUS *Habrocerus* ERICHSON, 1839

Within the Habrocerinae the genus *Habrocerus* is characterized by the shape of the antennae, the mouthparts and structure of the male genital segments (see below).

The last to describe a species of *Habrocerus* was PACE (1987) according to whom the genus then included four species: *H. magnus* Leconte and *H. schwarzi* Horn from North America, *H. capillaricornis* (Gravenhorst) from Europe (also introduced in North and South America) and the new species *H. rougemonti* Pace from Thailand. A fifth species, *H. tropicus*, had been described by WENDELER (1956) from Brazil. KORGE (1971) described a subspecies (*pisidicus*) of *H. capillaricornis* from Turkey. It might be worth mentioning that it was specimens of this subspecies, collected by the present authors in Turkey, which somehow raised our interest in the genus and mysteriously led to a worldwide revision.

MORPHOLOGY

Within the Staphylinidae *Habrocerus* is readily recognized by its *Tachyporus*-like body shape (and size), the more or less shining and non-pubescent surface of head, pronotum and elytra and a combination of various further traits (for further details see BLACKWELDER 1936; COIFFAIT 1972; LOHSE 1964). It differs from the only

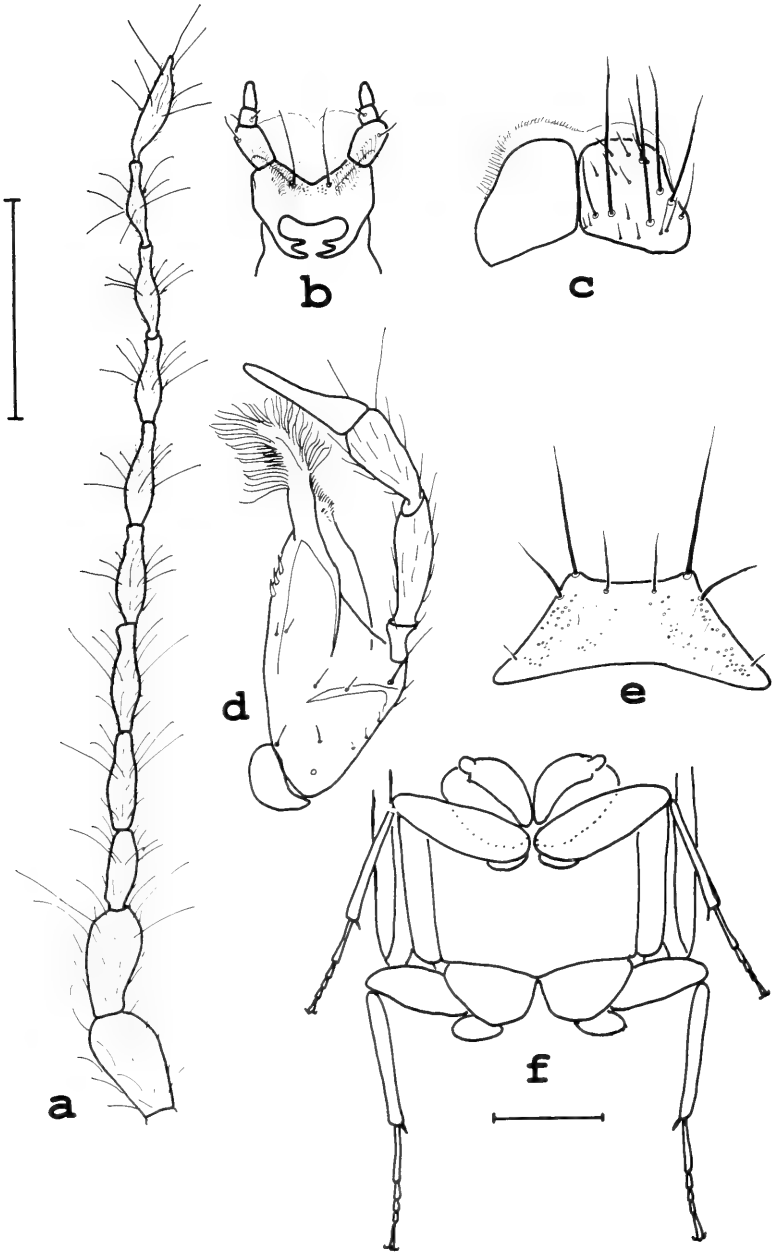


FIG. 1a-f

Habrocerus pisidicus Korge: antenna (a); labium (b); labrum (c); maxillary palpus (d); mentum (e); metathorax in ventral view (f). Scale: 0.5 mm.

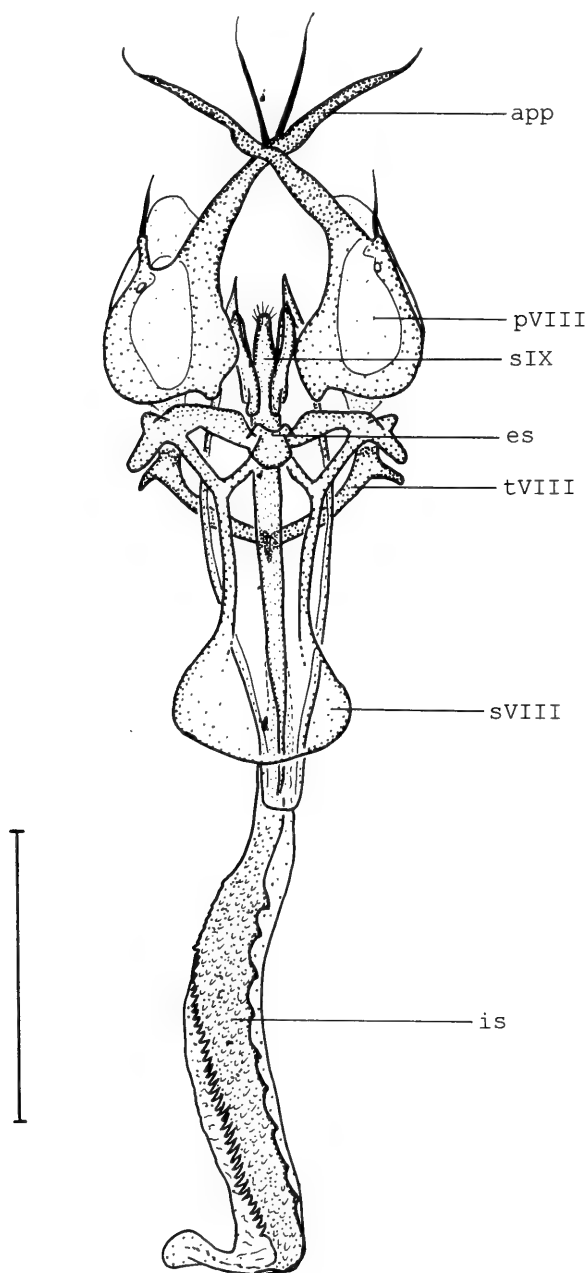


FIG. 2

Habrocerus pisidicus Korge: morphology of the ♂ urites VIII and IX in ventral view (app = appendices of pleurite VIII; es = emargination of central hind margin of sternite VIII; is = internal sac; pVIII = pleurite VIII; sVIII = sternite VIII; sIX = sclerites of urites IX; tVIII = tergite VIII. Scale: 0.5 mm.

further habrocerine genus *Nomimocerus* Coiffait & Saiz in that the antennomeres 3-11 are filiform in *Habrocerus* (Fig. 1a), whereas they are of normal shape and about the same width as segments 1-2 in *Nomimocerus* (Fig. 19a). Furthermore, the labial palpi are 3-segmented in the former and 4-segmented in the latter (COIFFAIT & SAIZ 1965) (Figs 1b, 19b). As in *Nomimocerus*, the maxillary palpi are 4-segmented (Fig. 1d). In contrast to most other Staphylinidae *Habrocerus* does not possess a ligula (Fig. 1b).

The most remarkable feature of *Habrocerus* is the structure of the abdominal segments VIII and IX, which are highly modified in the males. In Staphylinidae the first two abdominal segments are generally more or less merged with the metanotum, segments III-VIII with their corresponding tergites are usually visible, the sclerites of segments IX and X are modified and subject to various degrees of reduction and, finally, the males possess an aedeagus. In *Habrocerus* males, however, while segments I-VII are pretty much in accordance with the usual staphylinid condition, segment VIII forms part of the genital armature and is normally completely retracted in the abdomen (except for the apices of two spine-like appendices of pleurites VIII) (Fig. 2). According to COIFFAIT (1972) and MUIR (1919) the dorsal sclerite, shaped like a wide open V, is homologous to tergite VIII and is connected laterally to two pleural plates (pleurites VIII) each with a spiracle and with a long spine-like process, hereafter referred to as 'appendix'. Ventrally the pleurites are connected with sternite VIII, a large plate which is more or less widened anteriorly and which has an emargination posteriorly. (Both the appendices and the form of anterior and posterior part of sternite VIII offer easily visible characters for identification.) Segment IX, too, is highly modified. It is "shaped like an oat" (MUIR 1919) and consists of two slightly curved lobes dorsally connected in a V-shaped piece; ventrally a small trident body is visible, which is attached to a rod-like structure (Fig. 2, 9i, 10i). In the *Habrocerus schwarzi* species group (see below) the sclerites of urite IX are arranged asymmetrically.

As opposed to other Staphylinidae, *Habrocerus* males do not have an aedeagus, but "in the place of the median lobe we find a membranous tube opening in the dorsal aspect of the small trilobe process, on the same membrane as the anus is situated" (MUIR 1919). The internal sac is comparatively large and covered with minute spines. In addition, it may contain one or more rows of relatively large dark spines, the size and number of which vary between species and, therefore, represent very useful differential characters for identification (Figs 11, 18). For a more detailed description of the general structure of the male abdomen in *Habrocerus* see BLACKWELDER (1936), COIFFAIT (1965; 1972) and particularly MUIR (1919). It should be noted that BLACKWELDER (1936) erroneously bases his comments (pp. 80-81) on *Habrocerus schwarzi* Horn; his illustration (p. 82) clearly refers to *H. capillarcornis* (Grav.) and not to *H. schwarzi*.

The structure of the female abdomen in principle resembles the typical staphylinid condition with the pygidium and the stylus-shaped processes of urite IX visible in normal position (Fig. 4g-i). The posterior margins of tergite and sternite VIII are of diagnostic value in some species.

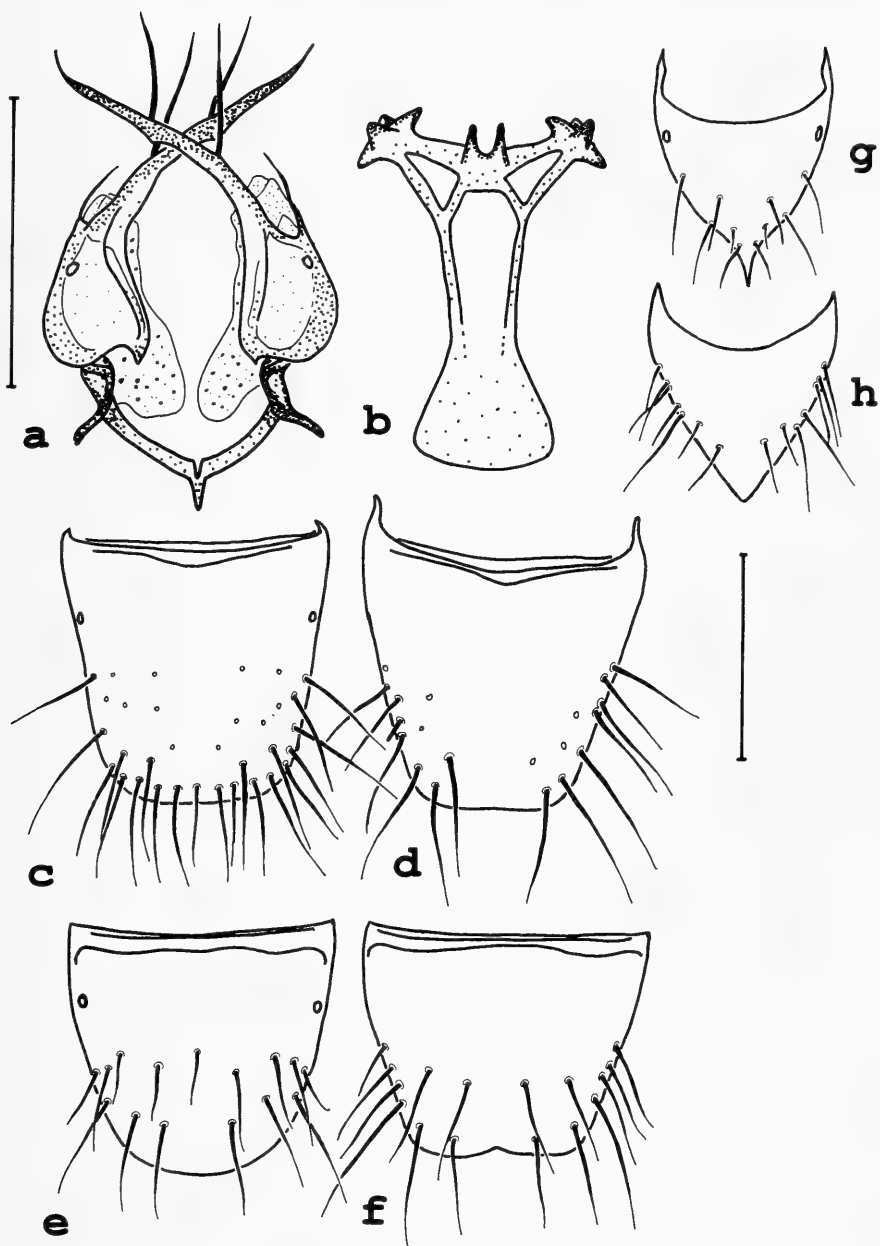


FIG. 3

Habrocerus capillaricornis (Gravenhorst): pleurites and tergite of ♂ urite VIII (a); ♂ sternite VIII (b); ♂ tergite VII (c); ♂ sternite VII (d); ♀ tergite VII (e); ♀ sternite VII (f); ♀ tergite VIII (g); ♀ sternite VIII (h). Scale: 0.5 mm.

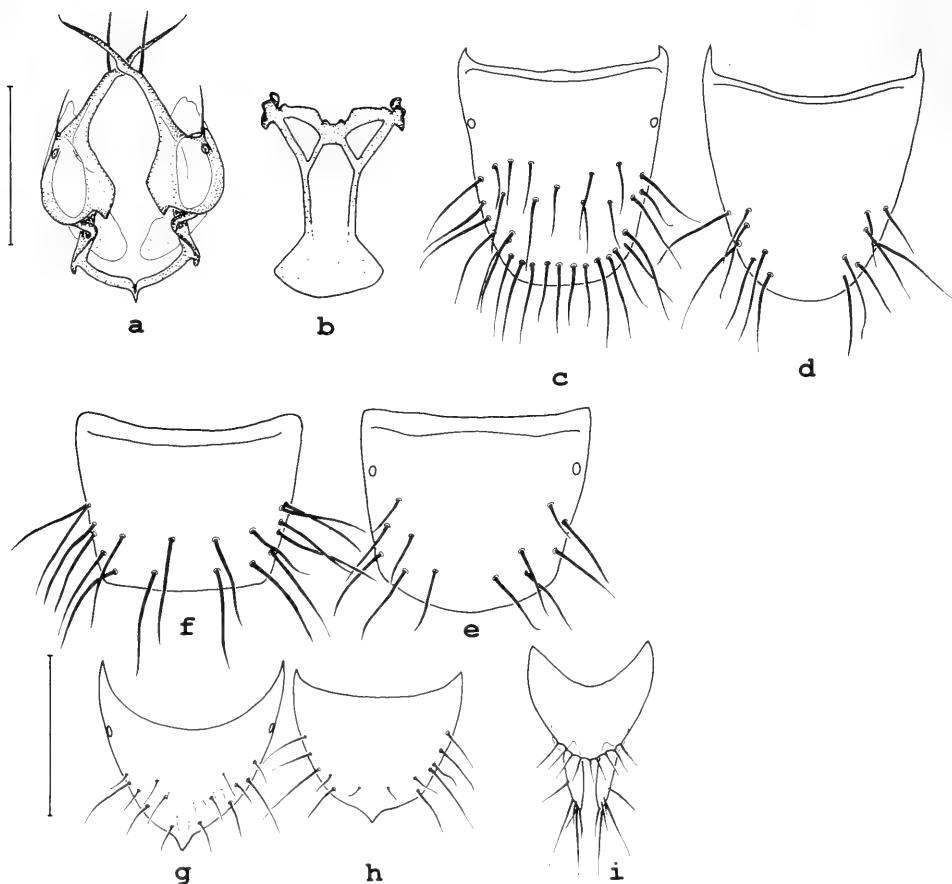


FIG. 4

Habrocerus pisidicus Korge: pleurites and tergite of ♂ urite VIII (a); ♂ sternite VIII (b); ♂ tergite VII (c); ♂ sternite VII (d); ♀ tergite VII (e); ♀ sternite VII (f); ♀ tergite VIII (g); ♀ sternite VIII (h); ♀ urite IX (i). Scale 0.5 mm.

THE SPECIES OF *Habrocerus*

The revision of several thousands of specimens of *Habrocerus* from our own material as well as from various private and museum collections yielded altogether 7 species new to science; 1 subspecies is raised to species rank. On the other hand it revealed that one of the four species known before our study must be excluded from the genus, so that *Habrocerus* currently comprises 13 valid species, seven of them Palaearctic, 3 Oriental, 1 Nearctic and 2 Neotropical. It may be assumed that a more intensive search especially in the Neotropical region and in Southeast Asia, perhaps also in other areas of the southern hemisphere (Australia, Africa) will lead to an increase in species number, since each of the 5 Neotropical and Oriental species is

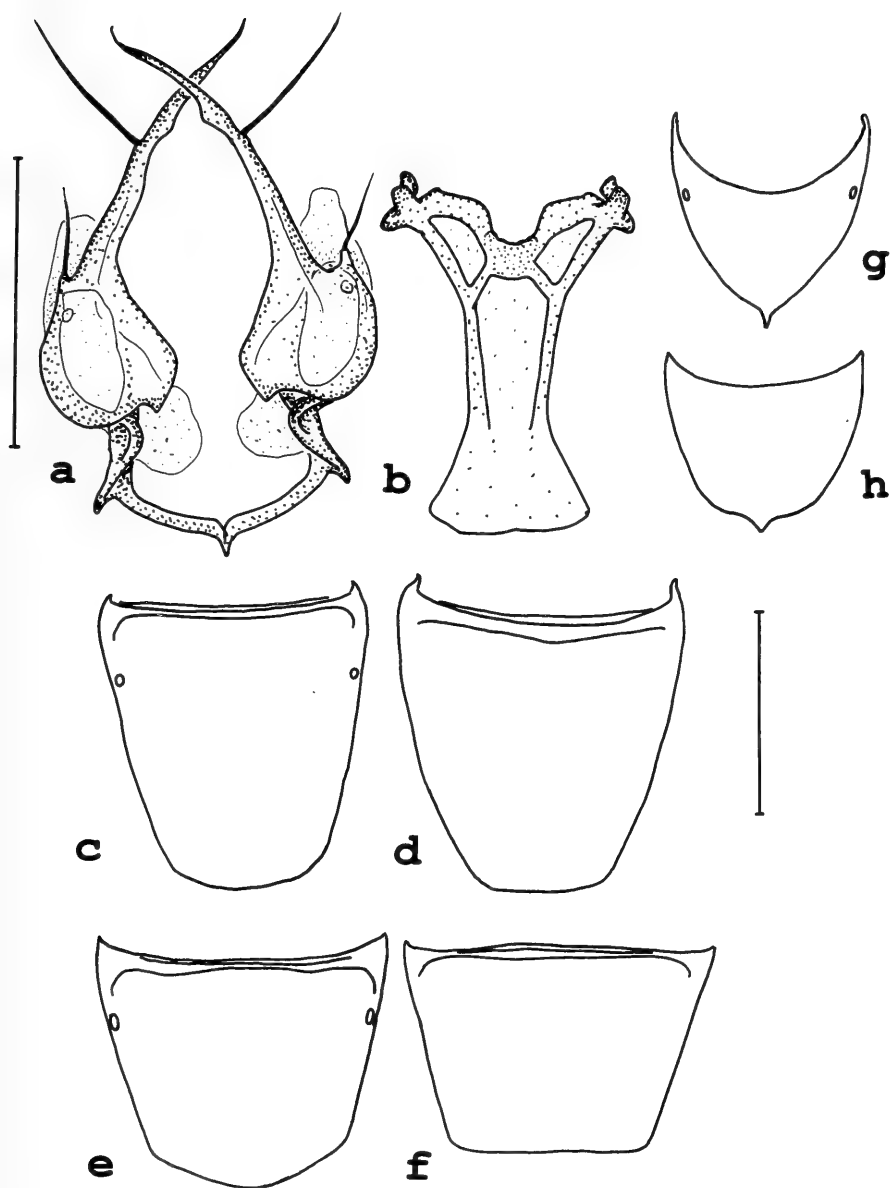


FIG. 5

Habrocerus simulans spec. nov.: ♂ pleurites and tegite of ♂ urite VIII (a); ♂ sternite VIII (b); ♂ tergite VII (c); ♂ sternite VII (d); ♀ tergite VII (e); ♀ sternite VII (f); ♀ tergite VIII (g); ♀ sternite VIII (h); setae and punctures omitted in c-h. Scale: 0.5 mm.

known only from one country or even one province. Hopefully, our study may also help to find *Habrocerus* material not yet revised from regions not yet covered.

Based on several characters, especially the morphology of the last segments of the abdomen in both males and females (see key), the genus *Habrocerus* can clearly be divided into three groups of species, hereafter referred to as the *Habrocerus capillaricornis* species group (with the exception of the presently wide-spread *H. capillaricornis* West Palaearctic), the *H. rougemonti* species group (Oriental) and the *H. schwarzi* species group (New World, East Palaearctic, Sumatra).

Since the species of *Habrocerus* within the species groups mentioned above, in some cases even between the groups, are usually highly similar in their external morphology, we consider it sufficient to give a detailed description of *H. capillaricornis* and relevant characters of typical representatives of the other groups. The descriptions of the remaining species will then focus on differential features. Therefore, the morphology of the internal sac and the posterior urites, particularly of the males, in some cases the only reliable characters for identification, is given special attention. For better evaluation of the number, sizes and shapes of the spines in the internal sac, the latter should be squeezed lightly and examined in transparent light under the microscope.

Chaetotaxy, an important means of identification in Tachyporinae (CAMPBELL 1979), may help to distinguish the species groups mentioned above, but has otherwise proved to be not very useful for separation of species within the groups. Not only are constant differences absent, many setae also tend to be missing in mounted material. Similarly, this applies to the antennae. Other characters are subject to various degrees of intraspecific variability, e.g. colour and microsculpture.

I. The *Habrocerus capillaricornis* species group

***Habrocerus capillaricornis* (Gravenhorst, 1806)**

Figs 3, 11, 12

Tachyporus capillaricornis Gravenhorst, 1806, *Mon. Col. Micr.*: 10f.

Tachyporus nodicornis Stephens, 1832, *Ill. Brit. Ent.* 5: 186f.

Habrocerus capillaricornis (Grav.), *Erichson*, 1839, *Käf. Mark Brandenb.* I: 401f.

LECTOTYPE: ♂, here designated, labels: Syn-Typus, Zool. Mus. Berlin,

Lectotypus, *Habrocerus capillaricornis* (Grav.), desig. Assing/Wunderle 1992 (MHB).

PARALECTOTYPES: 1 ♂, 1 ♀, here designated, labels as in lectotype; 1 ♀, here designated, labels: 5704, Syn-Typus, *capillaricornis*, Zool. Mus. Berlin (MHB).

FURTHER MATERIAL STUDIED:

A total of 2049 specimens from the following collections was studied: CsSch, BMNH, BRI, DEI, FMNH, MHB, MHNG, MNS, Czan, Cass, Cwun.

Europe: Germany (830), Austria (13), Switzerland (13), Poland (1), France (Continental: 45, Corse: 3), Spain (Continental: 92, Canary Islands: Tenerife: 11, La Palma: 137, Gomera: 5), Portugal (Continental: 16, Madeira: 8), Italy (Continental: 65; Sardinia: 1, Sicily: 6), CSFR (6), Hungary (5), Yugoslavia (33), Romania (8), Bulgaria (6), Greece (Continental: 14, Corfu: 8, Levkas: 10, Euboea: 1, Peloponnes: 5), Russia (1), Ukraine (2).

Asia: Turkey (15), Transcaucasia (?) (1).

North Africa: Algeria (62), Maroc (2).

North America: U.S.A. (519), Canada (93), South America: Colombia (2).

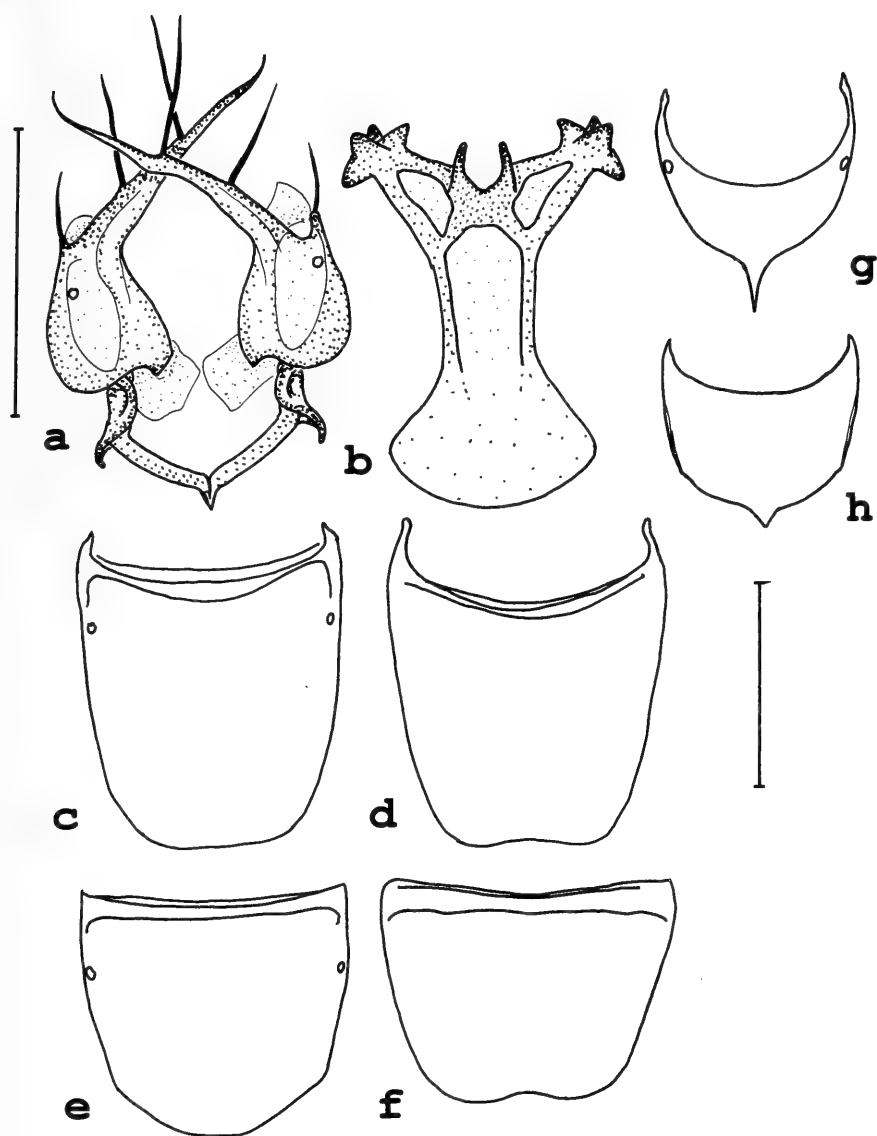


FIG. 6

Habrocerus cyprensis spec. nov.: ♂ pleurites and tergite of ♂ urite VIII (a); ♂ sternite VIII (b); ♂ tergite VII (c); ♂ sternite VII (d); ♀ tergite VII (e); ♀ sternite VII (f); ♀ tergite VIII (g); ♀ sternite VIII (h); setae and punctures omitted in c-h. Scale: 0.5 mm.

DESCRIPTION:

3.0-4.0 mm. Colour variable; head, pronotum and elytra light to pitchy brown, abdomen usually slightly darker except for the hind margins of the tergites; legs, antennae and mouthparts yellowish brown to light brown, maxillary palpi darkened.

Head with large eyes, in normal position reaching anterior margin of pronotum; surface shining, shallow transverse microsculpture only visible at higher magnifications (80x). Antennal segments 3-11 filiform, distinctly narrower than first two segments; segments 4-11 with short pubescence, a bottle-like dilatation and a circle of long setae in the middle (cf. Fig. 1a).

Pronotum ca. 1.5x wider than long, with arcuate sides converging more strongly anteriorly than posteriorly and with rounded angles; front and hind margin with 4, lateral margins with 2 long setae; epipleurae not visible in lateral view; disc of pronotum usually smooth and shining, superficial transverse microsculpture, if any, restricted to marginal areas of pronotal surface.

Elytra transverse, ca. 1.5x wider than long, at base about as wide as and at suture as long as pronotum; lateral margins slightly diverging posteriorly, hind angles truncate; elytra with 1 subhumeral seta, 2 setae near lateral margin and 1 seta at sutural angle; surface with often very weak micropunctuation and fine transverse microsculpture, its intervals clearly wider than those on the pronotum; epipleurae meeting with dorsal surface at acute angle.

Legs moderately long; apices of middle and hind femora with a long seta; tarsi 5-segmented; basal segment of middle and hind tarsi elongate, as long as the two following segments together, segments 2-4 decreasing in length, segment 5 as long as the two preceding ones together.

Abdomen with distinct lateral margins converging posteriorly, tergites with barely visible microsculpture and dense yellowish pubescence, their hind margins with long setae increasing in number caudally.

♂: appendices of pleurites VIII with 2 long setae (Fig. 3a), emargination of sternite VIII U-shaped and with relatively long posterior processes (Fig. 3b), hind margins of tergite and sternite VII straight with rounded angles (Figs 3c-d); internal sac with 6 large, wide-based spines and additional small sclerotized structures of roughly triangular shape (Fig. 11a).

♀: hind margin of tergite VII rounded, that of the corresponding sternite with shallow central emargination; tergite VIII acutely pointed (Fig. 3g), sternite VIII V-shaped (Fig. 3h) posteriorly.

DISTRIBUTION:

H. capillaricornis is widely distributed in the Western Palaearctic region. It is a common species in Central Europe and has also been recorded from the southern parts of the Scandinavian countries, from the British Isles (except Scotland), from southern Europe and the Mediterranean (including North Africa), eastern Europe and the Caucasus (Fig. 12). We have not seen any specimens from Cyprus, Rhodos and Crete.

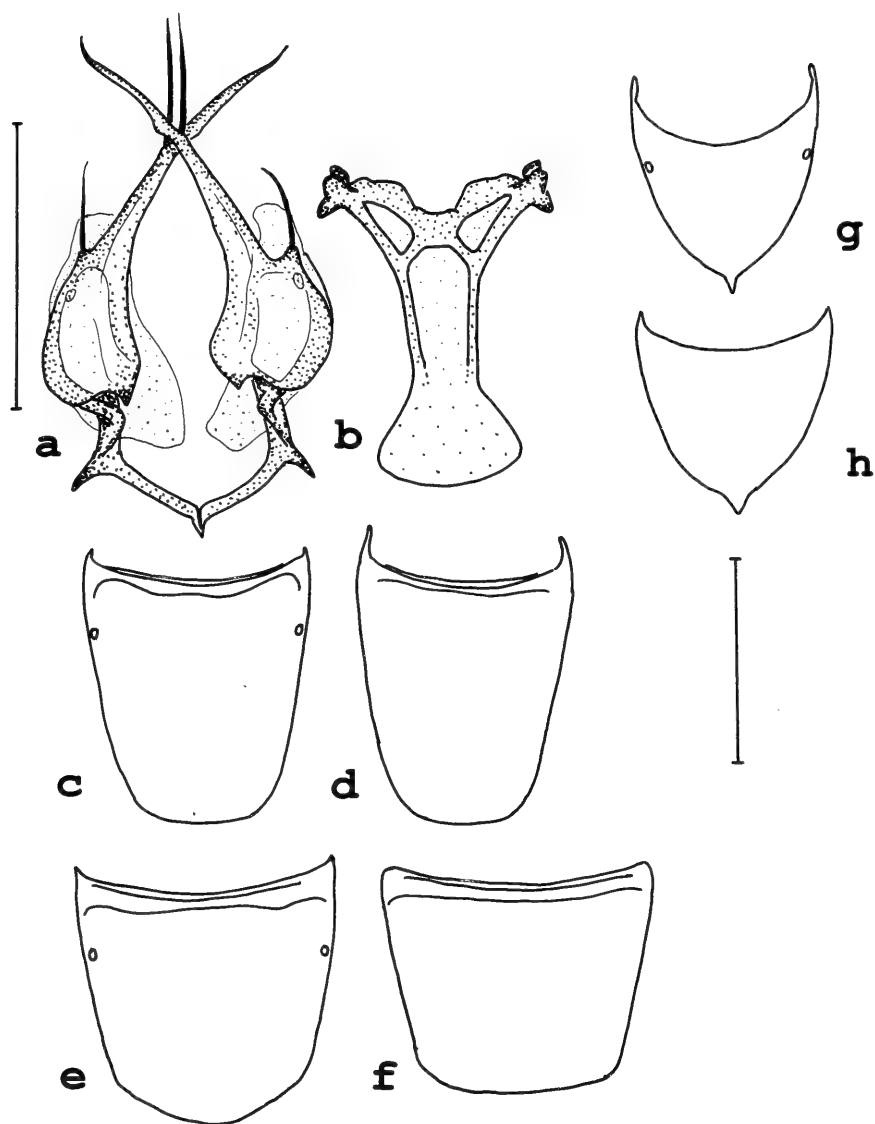


FIG. 7

Habrocerus ibericus spec. nov.: ♂ pleurites and tergite of ♂ urite VIII (a); ♂ sternite VIII (b); ♂ tergite VII (c); ♂ sternite VII (d); ♀ tergite VII (e); ♀ sternite VII (f); ♀ tergite VIII (g); ♀ sternite VIII (h); setae and punctures omitted in c-h. Scale: 0.5 mm.

According to the records known to us, *H. capillaricornis* occurs together with other congeneric species only in the Canary Islands (*H. canariensis* sp. n.) in south-west Europe (*H. ibericus* sp. n.), in Yugoslavia, Bulgaria, Greece and the Caucasus (*H. pisidicus*), whereas in most of Europe (northern and central European countries) it is the sole species present.

H. capillaricornis appears to have been introduced into North America in the late 1920s or the early 1930s. To our knowledge the first record dates back to 1931. The specimens (2 ♂♂) were collected in Natick, Massachusetts (Frost leg.), an island off Boston harbour. Subsequently, 1 ♀ was collected in Framingham Mass., ca. 20 mi. west of Boston harbour in 1934 and another ♀ in Sherbon, Mass., in 1935. In the following years the species must have spread over the states bordering on the Great Lakes, since it was first recorded from Indiana in 1943, from Illinois in 1958, from Wisconsin in 1953, from Ontario in 1951 and Quebec in 1956. Today it is known from practically all the states of the northeastern U.S. including the Great Lake area, from the southeast (Florida) and from southeastern Canada including Newfoundland. The first observation from the western U.S. dates back to 1941 in Oregon (2 ♂♂, Fender leg. (FMNH)) from where it was also recorded in the early 1940s by HATCH (1957) (SMETANA, pers. comm.). Since then the species has also been collected in California, Kansas (1942!) and Nebraska. These data seem to suggest that *H. capillaricornis* was introduced into North America at least twice, first at the East Coast (very probably Boston, Mass.), then at the West Coast.

We have seen 2 ♂♂ from Lago de Tota in Colombia, South America, which were collected at an altitude of 3000-3700 m (C. Reid leg., 1982; BMNH). According to HAMMOND (pers. comm.) the species is also known to occur in New Zealand.

BIONOMICS:

H. capillaricornis inhabits all kinds of detritus (leaf litter, fungi, under bark, etc.), especially in woodland at lower altitudes. According to HORION (1967) adult beetles are collected from March through May and from September through December. A pitfall trap study in two forests near Hannover, Germany (ASSING, unpubl.) and further collection data revealed, in contrast, that *H. capillaricornis* adults are present throughout the year, the highest locomotive activity taking place in spring (April through June). Above-ground activity was even recorded in December and January, when the temperature conditions were suitable. Data on the egg-laying period are scarce. 4 females were found to have mature eggs in their gonads in June. In Northwest Germany, immature adults were recorded in September (ASSING, unpubl.).

These results would indicate a univoltine life-cycle with an egg-laying period in spring, larval and pupal development in summer and the following generation of adults emerging from the pupae in autumn and overwintering before reproducing again in spring. However, the phenology of *H. capillaricornis* may not be quite that simple. In France, south of the Loire, PAULIAN (1941) collected a larva in April, 1938. The pupal development (pupa libra) lasted from April 24 to May 7, 1938. Near Firenze, Italy, 1 immature ♂ was collected on June 15 (Assing leg.), in Southern Spain (Ronda) 2 immature ♂♂ were sampled on March 26, and on Tenerife, Canary

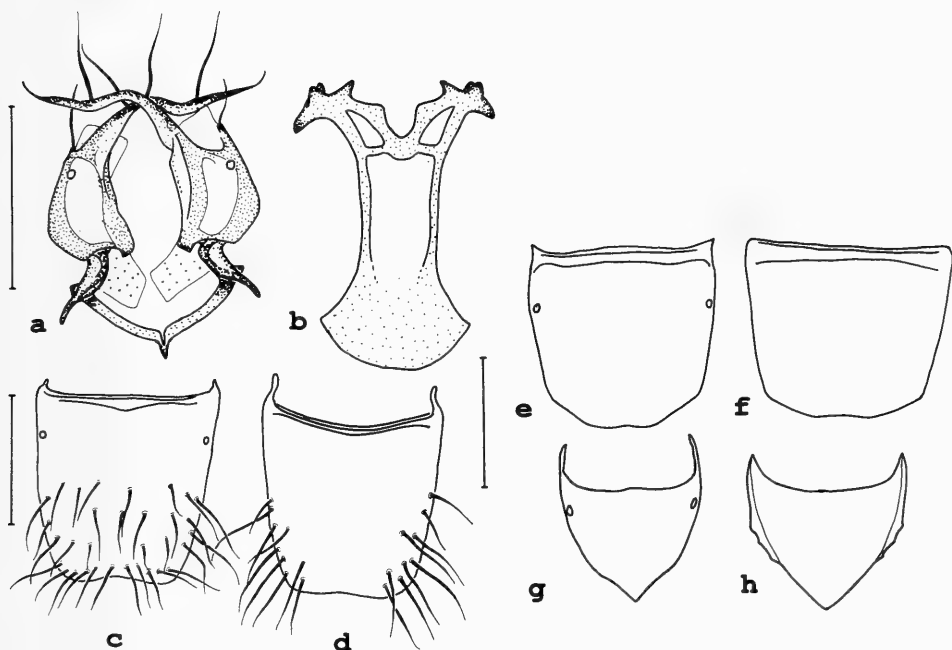


FIG. 8

Habrocerus canariensis spec. nov.: pleurites and tergite of ♂ urite VIII (a); ♂ sternite VIII (b); ♂ tergite VII (c); ♂ sternite VII (d); ♀ tergite VII (e); ♀ sternite VII (f); ♀ tergite VIII (g); ♀ sternite VIII (h); setae and puncture omitted in e-h. Scale: 0.5 mm.

Islands, 5 teneral specimens (Assing leg.) were observed on April 14. Thus, the phenology of *H. capillaricornis* seems to be strongly dependent on climatic conditions. The data from Southern Europe and the Canary Islands may even suggest a bi- or perhaps polyvoltine life-cycle. However, more material and studies are needed before drawing any further conclusions.

According to observations in Albania (HORION 1967) and in the surroundings of Hannover, Germany (ASSING, unpubl.) dispersal by flight seems to take place from April to June. On one occasion in May 1992 as many as 169 flying *Habrocerus* were collected with a car-net in 30 minutes (Hannover).

Descriptions of the larva of *H. capillaricornis* can be found in GANGLBAUER (1895) and PAULIAN (1941).

***Habrocerus pisidicus* Korge, 1971, stat. nov.**

Figs 1, 2, 4, 11, 12

Habrocerus capillaricornis ssp. *pisidicus* Korge, 1971, *Ann. Zool. Bot.* No. 67/ 58f.

HOLOTYPE: ♂, Anatolia mer., Korge & Heinze leg., Pisid. Taurus, Bozburun 1600-2000 m, 20.VII.65 (Ckor).

FURTHER MATERIAL STUDIED:

Bosnia: (11) (DEI, Cass, Cwun).

Bulgaria: Rhodope (4) (DEI, NHMW).

Greece: Ipeiros (74) (MHNG), Crete (46) (MHNG, Cwun), Rhodos (72) (MHNG), Corfou (36) (MHNG, Ckat, Cwun), Cephallonia (13) (MHNG), Levkas (135) (MHNG, Cass), Peloponnes (1) (NHMW).

Cyprus: (58) (MHNG).

Turkey: Thrace (19) (Ckor), Central (3) (MHNG), Southwest (110) (Ckor, MHNG, NHMW, Cass, Cwun); Northwest (44) (MHNG, NHMW).

Transcaucasia? (identification uncertain): Georgia (3 ♀ ♀) (Csch).

DESCRIPTION:

3.0-4.0 mm. Size and body proportions as in *H. capillaricornis*. Colour, especially of head, pronotum and elytra, usually slightly darker than in *H. capillaricornis*, dark brown to pitchy brown.

Pronotum with the whole surface generally covered with fine transverse microsculpture. Setae, punctuation and shape of pronotum and elytra as in *H. capillaricornis*. Elytral microsculpture frequently more distinct.

Appendages and first abdominal segments similar to *H. capillaricornis*.

♂: hind margin of tergite VII almost straight with rounded angles (Fig. 4c), that of sternite VII ± rounded (Fig. 4d); appendices of pleurites VIII with 1 long seta (Fig. 4a), central emargination of sternite VIII broad with short posterior processes (Fig. 4b); internal sac with a row of ca. 11 large spines of elongate triangular shape (Fig. 11c).

♀: tergite VII with weakly rounded, sternite VII with almost straight hind margin (Figs 4e-f); tergite and sternite VIII shortly pointed posteriorly (Figs 4g-h).

DISTRIBUTION:

H. pisidicus has been recorded from Turkey (Thrace; northern, western and central parts of Anatolia), from Greece (including Crete and islands), Cyprus, Bulgaria and Bosnia. The records from Transcaucasia (only ♀ ♀) remain doubtful. The species was observed to occur together with *H. capillaricornis* in Bosnia, Greece (Levkas, Corfou, Epire) and the European part of Turkey and together with *H. cyprensis* on Cyprus (Fig. 12).

BIONOMICS:

Little is known about the bionomics of *H. pisidicus*. It has been collected over a wide range of altitudes (50 - ca. 1800 m) in various kinds of litter, frequently together with *H. capillaricornis*, in December, January and from April through September. Teneral specimens were observed in April, May, July and August.

ADDENDUM:

After the manuscript had gone to press, *H. pisidicus* was also recorded from Southern Italy: 22♂♂, 20♀♀, Mte. Gargano (various localities), in stands of *Quercus* spp., 400-900m, 30.XII.1994, leg. & coll. Assing; 3♂♂, 1♀, Puglia, Martina (TA), 17.XII.89, leg. & coll. Montemurro.

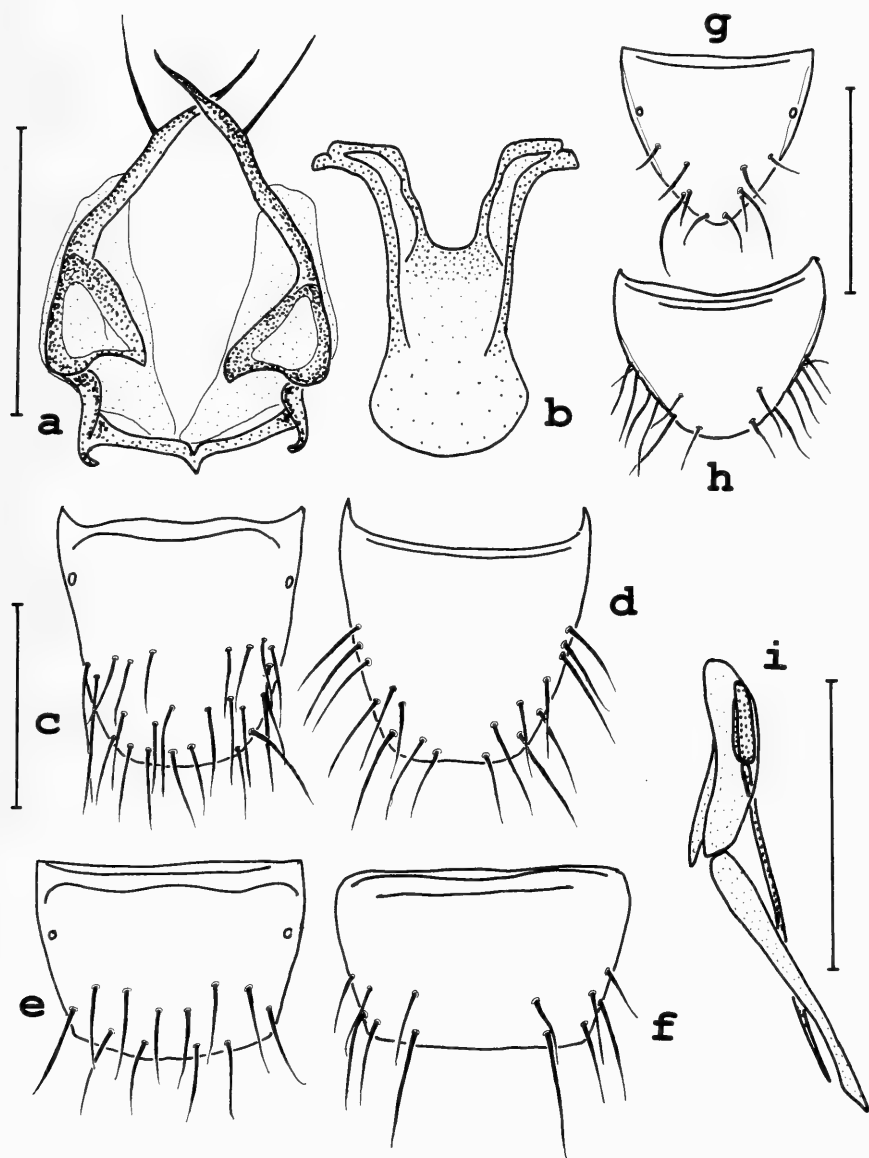


FIG. 9

Habrocerus rougemonti Pace: ♂ pleurites and tergite VIII (a); ♂ sternite VIII (b); ♂ tergite VII (c); ♂ sternite VII (d); ♀ tergite VII (e); ♀ sternite VII (f); ♀ tergite VIII (g); ♀ sternite VIII (h); ♂ urite IX in lateral view (i). Scale: 0.5 mm.

Habrocerus simulans spec. nov.

Figs 5, 11, 12

HOLOTYPE: ♂; labels: Israel, Coté Mt Carmel, 100 m, 17.IV.1982, Besuchet & Löbl (MHNG).

PARATYPES: *Israel*: 54 ♂♂, 50 ♀♀: same data as holotype; 17 ♂♂, 32 ♀♀: Mt Carmel, Little Switzerland, 28.V.73; 34 ♂♂, 27 ♀♀: Galilée, au-dessous Safad, 500 m, 30.V.73, Löbl; 12 ♂♂, 12 ♀♀: Galilée, Eilon N Betzel, 20.IV.82, Besuchet & Löbl; 16 ♂♂, 10 ♀♀: Galilée, Montefort, 19.IV.82, Besuchet & Löbl; 4 ♂♂, 2 ♀♀: Galilée, Mt Meron, 900-1000 m, 27.V.72, Löbl; 1 ♂, 3 ♀♀: Galilée, Mt Meron, 700 m, 26.IV.82, Besuchet & Löbl; 1 ♂: Galilée Tel Dan, 24.IV.82, Besuchet & Löbl; 1 ♂: Golan, Gilbon, 300 m, 15.IV.82, Besuchet & Löbl; 1 ♀: Golan, Banias, 24.IV.82, Besuchet & Löbl; 1 ♀: Coté Akko, N Naaman, 18.IV.82, Besuchet & Löbl (MHNG, Cass, Cwun).

Lebanon: 5 ♂♂, 8 ♀♀: Jeita, 26.III.75, Besuchet; 6 ♂♂, 6 ♀♀: env. Damour, 28.III.75, Besuchet (MHNG, Cass, Cwun).

Turkey: 2 ♀♀: Artvin, Pirnalli, Massif du Karkal Dagi, 1600 m, 11.IV.86. 7 ♂♂, 10 ♀♀: Artvin, Pirnalli, Massif du Karkal Dagi, 1250 m, 11.IV.86; 3 ♂♂, 3 ♀♀: Artvin, s/Artvin, 800 m, 7.VI.86, Besuchet, Burckhardt & Löbl; 10 ♂♂, 3 ♀♀: Mersin, Tarsus, Gülek, 1550 m, 30.IV.78, Besuchet; 7 ♂♂, 2 ♀♀: Tokat-Almus, 1200 m, 21.IV.67, Besuchet; 1 ♀: Adana, Kozan, 5.V.67, Besuchet; 13 ♂♂, 14 ♀♀: Antakya, 400-850 m, V.78, Besuchet & Löbl (MHNG, Cass, Cwun).

DESCRIPTION:

Size, body proportions, setae, punctation and colour as in *H. capillaricornis*.

Pronotum with fine transverse microsculpture on whole surface (as in *H. pisidicus*).

♂: hind margins tergite and sternite VII nearly straight to weakly rounded (Figs 5c-d); appendices of pleurites VIII with one long seta (as in *H. pisidicus*) (Fig. 5a); emargination of sternite VIII broad and U-shaped, posterior processes very indistinct (Fig. 5b); internal sac with 5-6 relatively large, elongate spines (Fig. 11d).

♀: tergites and sternites VII and VIII as in *H. pisidicus* (Figs 5e-h).

DISTRIBUTION:

H. simulans is widely distributed in the Eastern Mediterranean region (Fig. 12). It has been recorded from Israel, Lebanon and East Anatolia, from where we have not seen any other species of *Habrocerus* yet.

BIONOMICS:

Ecological data are scarce. *H. simulans* apparently inhabits a wide range of altitudes (100-1600 m). Immature specimens were found in March and April.

Habrocerus cyprensis spec. nov.

Figs 6, 11, 12

HOLOTYPE ♂; labels: Chypre, Baths of Aphrodite, 22.VII.77, C. Besuchet (MHNG).

PARATYPES: 11 ♂♂, 7 ♀♀: same data as holotype; 5 ♂♂, 2 ♀♀: Chypre, Yerowasa, 14.VII.77, C. Besuchet; 1 ♂, 6 ♀♀: Chypre, Ayios Dhimitrios, 600 m, 9.VII.77; 2 ♂♂, 1 ♀: Chypre,

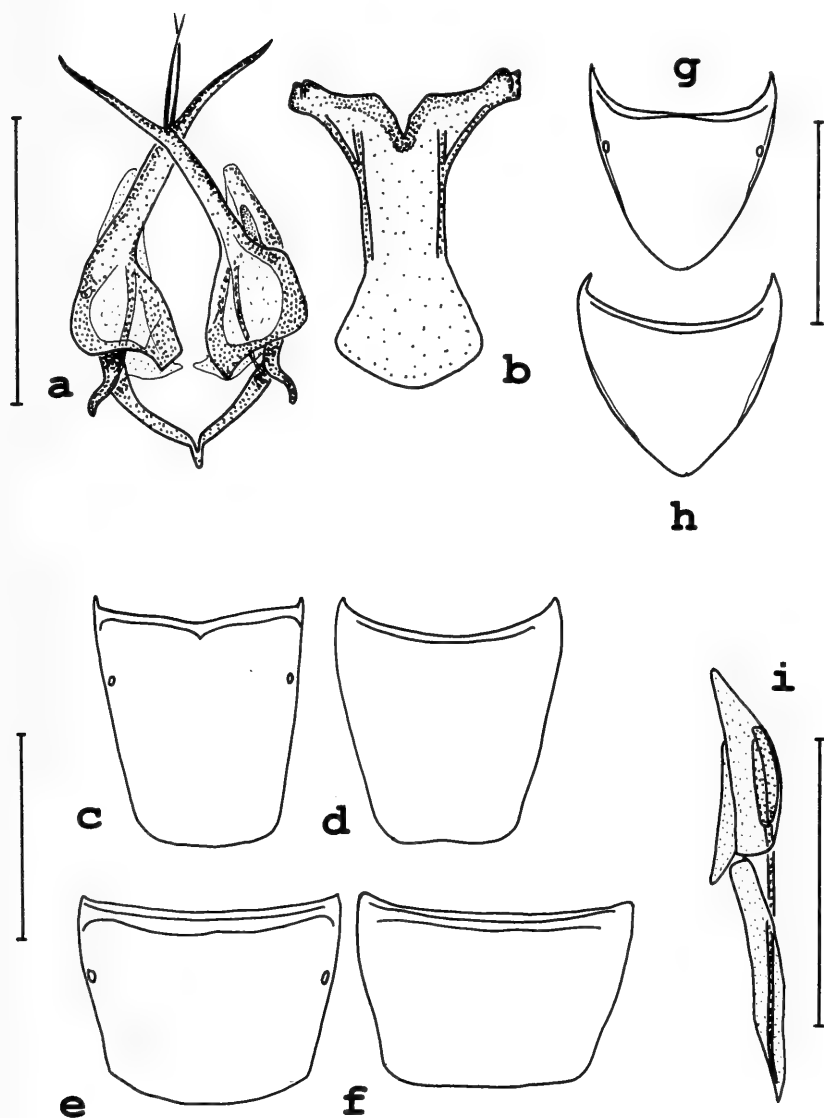


FIG. 10

Habrocerus indicus spec. nov.: ♂ pleurites and tergite VIII (a); ♂ sternite VIII (b); ♂ tergite VII (c); ♂ sternite VII (d); ♀ tergite VII (e); ♀ sternite VII (f); ♀ tergite VIII (g); ♀ sternite VIII (h); ♂ urite IX in lateral view (i); setae and punctures omitted in c-h. Scale: 0.5 mm.

Mamonia, 14.VII.77, C. Besuchet; 2 ♂♂, 1 ♀: Chypre, Stroumbi, 400 m, 22.VII.77, C. Besuchet; 1 ♂: Chypre, Caledonian Falls, 1400 m, 1.VII.77, C. Besuchet; 1 ♂: Chypre, V. de Cédres, 1200 m, 12.VII.77, C. Besuchet (MHNG, Cass, Cwun).

DESCRIPTION:

Size, body proportions, setae, punctation, microsculpture and colour as in *H. capillaricornis*.

♂: tergite VII with nearly straight, sternite VII with shallowly concave hind margin (Figs 6c-d); appendices of pleurites VIII with 2 setae (Fig. 6a); central emargination of sternite VIII similar to *H. capillaricornis*, but broader and with longer, slightly converging posterior process (Fig. 6b); internal sac without dark spines (Fig. 11f).

♀: tergite VII rounded, the corresponding sternite shallowly concave posteriorly (Figs 6e-f); acutely pointed process of hind margin of tergite VIII longer than in *H. capillaricornis* (Fig. 6g); sternite VIII shortly pointed posteriorly (similar to *H. pisidicus*) (Fig. 6h).

DISTRIBUTION:

H. cyprensis appears to be endemic to Cyprus (Fig. 12).

BIONOMICS:

The species apparently inhabits a wide range of altitudes. At several localities it was collected together with *H. pisidicus*.

***Habrocera ibericus* spec. nov.**

Figs 7, 11, 12

HOLOTYPE: ♂, Portugal, Algarve, 8 km N S. Brás de Alportel, 400 m, 1.VI.92, Wunderle (Cwun).

PARATYPES: 22 ♂♂, 18 ♀♀: same locality as holotype, 29.V.-4.VI.92 (Cass, Cwun); 2 ♂♂, 1 ♀: Gallia merid., Ste. Maxime Var., 26.III.13, W. Liebmann (DEI); 1 ♂: E., La Iruela, Jaen, Queva segreta del Sagrio, 30.III.87, Zoia leg. (Czan); 1 ♂: E., Castellon de la Plana, env. Cabanes, 320 m, 19.III.87, Zoia leg. (Czan); 1 ♂: E., Algeciras, Cadiz, Sierra del Nino, 180 m, 26.III.87, Zoia leg. (Czan); 7 ♂♂, 5 ♀♀: Espagne, Castellon, Querol près Morella, 5.V.66, Besuchet (MHNG, Cass, Cwun); 1 ♂: Sierra Guadarrama, Spain, H. Franz leg. (NHMW); 1 ♀: Espagne, Huelva, Agua Fria près Jabugo, 3.VI.66, Besuchet (MHNG); 1 ♂: Espagne, Castellon, Cáliz près Benicarlo, 6.V.66, Besuchet (MHNG); 1 ♂: Espagne, Cuenca Las Torcas, 19.V.60, Besuchet (MHNG); 1 ♂, 2 ♀♀: Espana, Provinz Cadiz, Algeciras, El Bujeo, 340 m, 13.IV.1983, leg. et coll. Elbert; 4 ♂♂, 2 ♀♀: E., Andalusien (GR), Sierra Nevada, Capileira, 1400 m, 23.III.1994, Assing & Wunderle leg. (Cass, Cwun); 1 ♂, 3 ♀♀: E., Andalusien (GR), Sierra Nevada, Lanjaron, 600 m, 23.III.1994, Assing leg. (Cass.); 2 ♂♂, 1 ♀: E., Andalusien (MA), Sierra de Palmitera, SO Ronda, 900 m, 24.III.1994, Assing leg. (Cass); 17 ♂♂, 7 ♀♀: E., Andalusien (CA), Umg. Algeciras, Sierra de Luna, 200 m, 28.III.1994, Assing & Wunderle leg. (Cass, Cwun); 4 ♂♂, 2 ♀♀: E., Andalusien (CA), Umg. Algeciras, Sierra de Luna, 350 m, 28.III.1994, Assing & Wunderle leg. (Cass, Cwun).

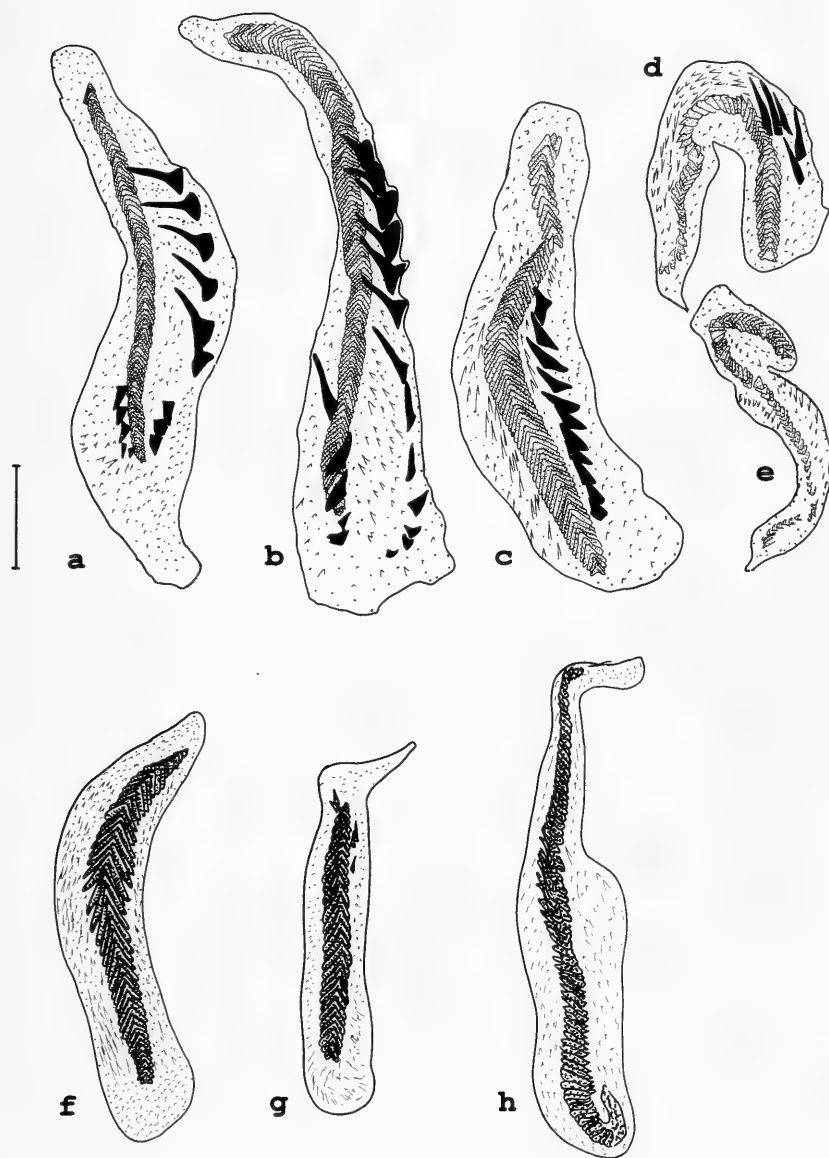


FIG. 11

The *Habrocerus capillaricornis*- and the *H. rougemonti*-group: Internal sacs of *H. capillaricornis* (a), *H. canariensis* (b), *H. pisidicus* (c), *H. simulans* (d), *H. ibericus* (e), *H. cyprensis* (f), *H. rougemonti* (g) and *H. indicus* (h). Scale: 0.25 mm.

DESCRIPTION:

Size, body proportions, setae, punctuation and colour as in *H. capillaricornis*.

Pronotum with fine transverse microsculpture on whole surface (as in *H. pisidicus*).

♂: tergite and sternite VII with nearly straight hind margin (as in *H. simulans*) (Figs 7c-d); appendices of pleurites VIII with one seta (Fig. 7a); emargination of sternite VIII broad and with very indistinct posterior processes (as in *H. simulans*) (Fig. 7b); internal sac small and without dark spines (Fig. 11e).

♀: tergites and sternites VII and VIII as in *H. simulans* (Figs 7e-h).

DISTRIBUTION:

According to the material available to us the area of distribution of *H. ibericus*, which apparently completely overlaps with a part of that of *H. capillaricornis*, ranges from the south of France to the south of Spain and Portugal. In addition to the records indicated above, 2 ♀♀ were collected in Cantabria in the northwest of Spain.

BIONOMICS:

H. ibericus was collected in leaf litter especially in stands of *Quercus suber* (Portugal, type locality; Spain, Algeciras) and *Qu. ilex* (Spain, Castellon de la Plana; Sierra Nevada; Sierra de Luna), but also in woodland composed of other trees, at altitudes of 180-1400 m. On several occasions, at the type locality, in the Sierra Nevada and in the Sierra de Luna the species was sieved together *H. capillaricornis*. Several immature adults were collected on March 28, 1994, near Algeciras, and one teneral specimen was taken in the middle of April.

Habrocerus canariensis spec. nov.

Figs 8, 11, 12

HOLOTYPE: ♂, E., La Gomera, El Cedro, 900 m, 2.XI.1990, Wunderle (Cwun).

PARATYPES: 4 ♂♂, 4 ♀♀: same data as holotype (Cass, Cwun); 2 ♂♂, 2 ♀♀: E., La Gomera, El Cedro, Erem. Nostra Sen., 1000 m, 27.-28.X.90 (Cwun); 1 ♂: La Gomera, El Cedro, 7.I.83, P. Oromi (MCNT); 1 ♀: Hierro, Manca Fite, 16.IV.84, P. Oromi (MCNT); 4 ♂♂, 1 ♀: Hierro, El Golfo, 800-1000 m, 8.III.83, Besuchet (MHNG); 2 ♂♂, 1 ♀: Gran Canaria, Barranco de Los Cernicalos, 19.VI.85, A. Aquiar (MCNT); 1 ♀ La Palma, S Gallegos, N-Seite, 1000 m, 11.III.84, Martens (MNS); 1 ♂, 2 ♀♀: La Palma, Los Tilos; 12.III.90, Schwaller (MNS); 1 ♀: Canaries, La Palma, La Galga, 7.IX.93 (Csch); 1 ♂, 4 ♀♀: Canaries, M. Cameron, 1955 (BMNH); 1 ♀: Canary Isl. (BMNH).

DESCRIPTION:

3.5-4.5 mm. Overall appearance almost bicoloured: head blackish brown; pronotum and abdomen, except for the hind margins of the tergites, brown; elytra lighter in colour, reddish brown, usually somewhat darkened in the posterior angles.

Body proportions, setae and punctuation, on the whole, similar to *H. capillaricornis*, but the abdomen has a slightly more parallel shape and the posterior angles of the elytra are more broadly truncate.

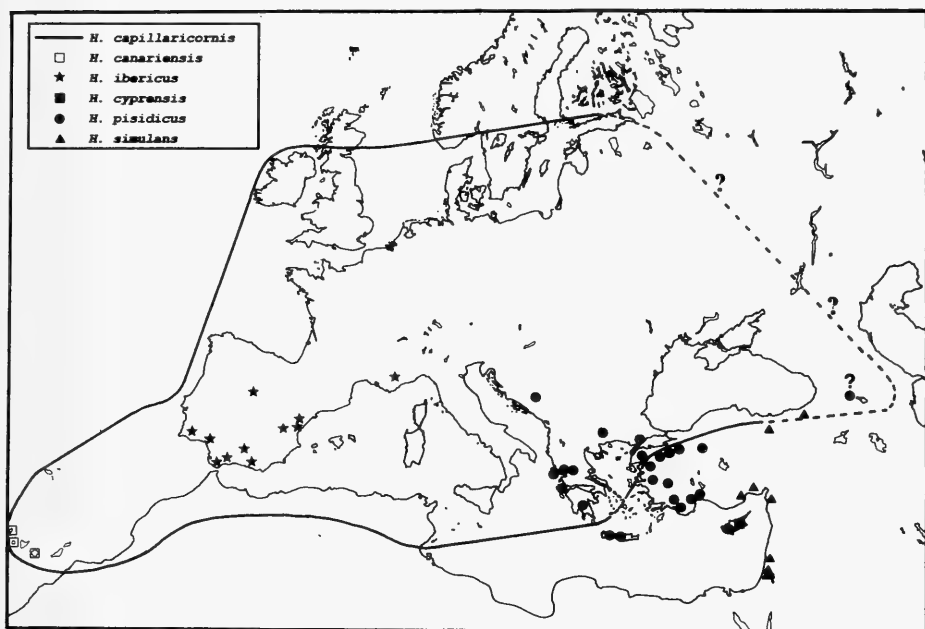


FIG. 12

Distribution of the species of *Habrocerus* in the Western Palearctic region.

♂: tergite and sternite VII with shallowly concave hind margins (Figs 8c-d); appendices of pleurites VIII strongly curved and with 2 long setae (Fig. 8a); emargination of sternite VIII deep and U-shaped, without posterior processes; anterior dilatation of sternite VIII angular (Fig. 8b); internal sac with 6 large and wide-based spines and several additional, mostly elongate spines of various shapes (Fig. 11b).

♀: tergite and sternite VII relatively broad with shallowly concave hind margins (Figs 8e-f); tergite and sternite VIII pointed, the latter with distinct setal insertions laterally (Figs 8g-h).

DISTRIBUTION:

H. canariensis is endemic to the Canary Islands (La Gomera, La Palma, Gran Canaria and Hierro), where it co-occurs with *H. capillaricornis* on La Palma and La Gomera.

BIONOMICS:

On La Gomera *H. canariensis* was sieved from *Laurus* leaf litter at higher altitudes (900-1000 m), where *H. capillaricornis* was absent. Adult specimens were observed in January, March, April, October and November.

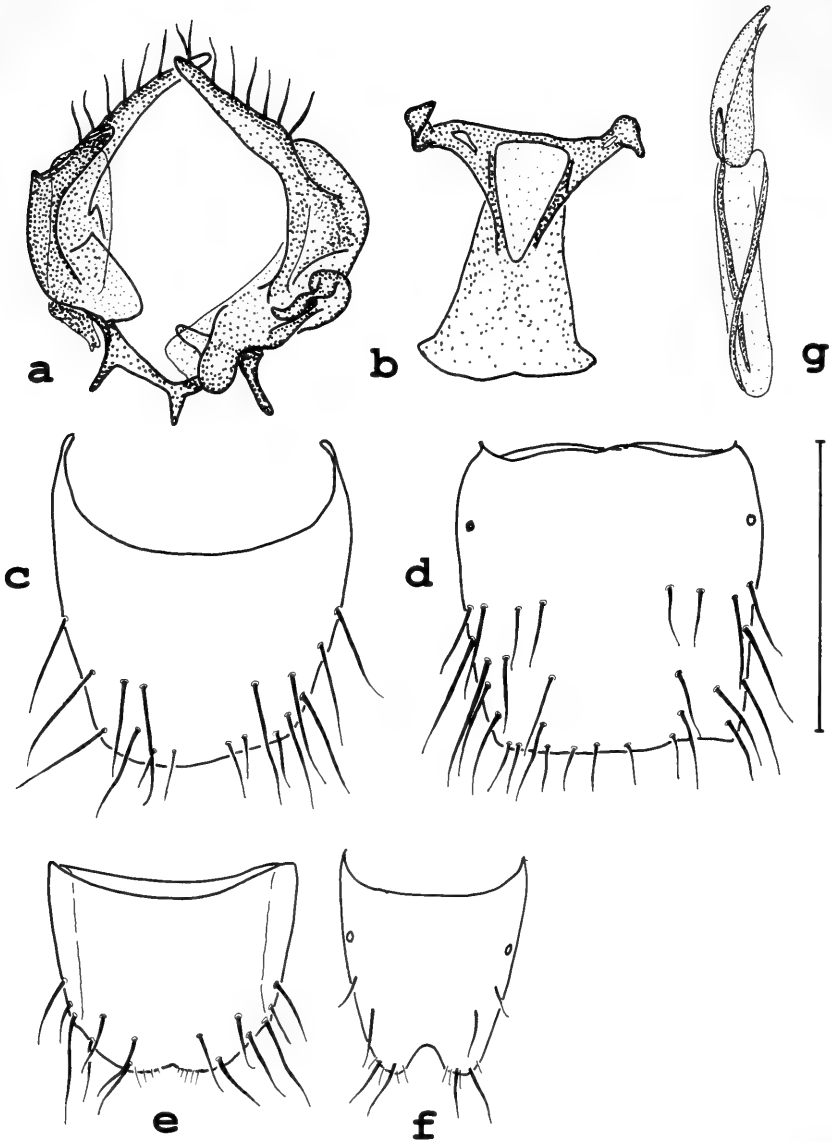


FIG. 13

Habrocerus schwarzi Horn: pleurites and tergite of ♂ urite VIII (a); ♂ sternite VIII (b); ♂ sternite VII (c); ♂ tergite VII (d); ♀ sternite VIII (e); ♀ tergite VIII (f); ♂ urite IX in lateral view (g). Scale: 0.5 mm.

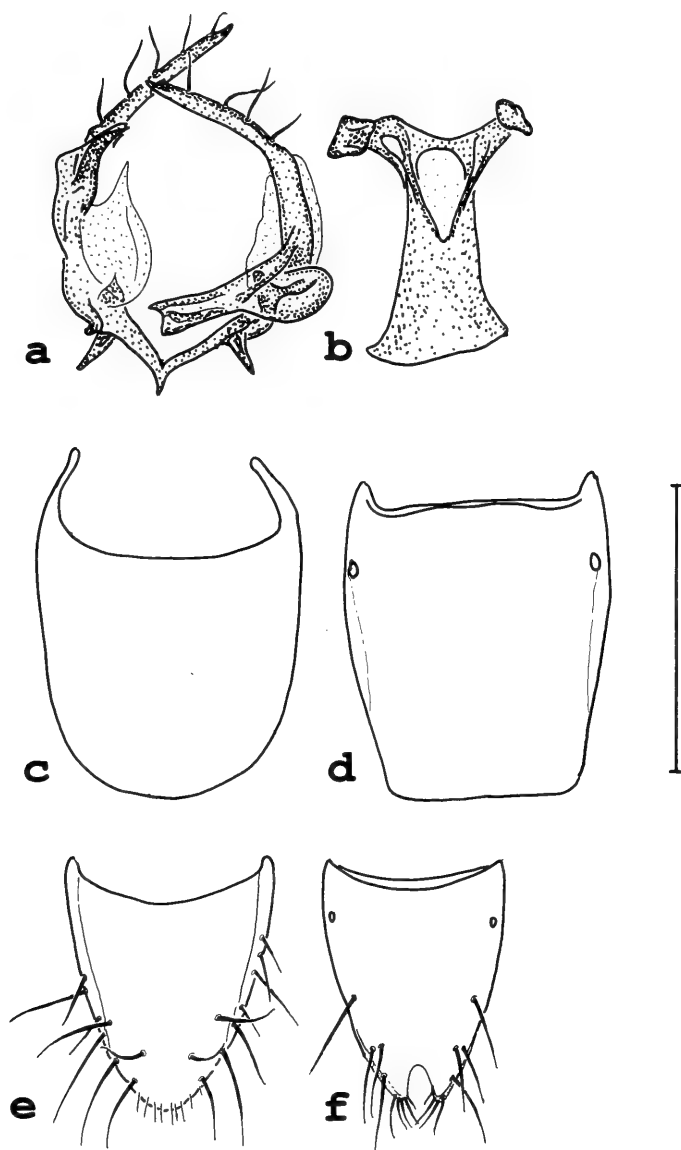


FIG. 14

Habrocerus tropicus Wendeler: pleurites and tergite of ♂ urite VIII (a); ♂ sternite VIII (b); ♂ sternite VII (c); ♂ tergite VII (d); ♀ sternite VIII (e); ♀ tergite VIII (f); setae and punctures omitted in c-d. Scale: 0.5 mm.

II. The *Habrocerus rougemonti* species group

Habrocerus rougemonti Pace, 1987

Figs 9, 11

Habrocerus rougemonti Pace 1987, *Elytron* 1: 5ff. figs.

HOLOTYPE: ♂, Thailand, Chiang Mai Prov., Doi Suthep, III.1987, leg. Rougemont (MCSNV).

FURTHER MATERIAL STUDIED:

Thailand: 13 ♂♂, 19 ♀♀: NE Bangkok, Khao Yai Nat. Park, Khao Khieo, 1150 m, Burckhardt & Löbl, 28.XI.85; 5 ♂♂, 6 ♀♀: Chiang Mai, Doi Inthanon, 1250 m, 6.XI.1985, Burckhardt & Löbl; 1 ♂: Prov. Chiang Mai, Doi Suthep, 1150 m, 14.I.87, P. Schwendinger; 3 ♂♂, 2 ♀♀: Prov. Chiang Mai, Doi Suthep, 1400 m, 5.XI.85, Burckhardt & Löbl; 3 ♂♂: Chiang Mai, Mar Nang Kao, 900 m, 54 km NE Chiang Mai, 3.XI.85, Burckhardt & Löbl (NHMG, Cass, Cwun).

DESCRIPTION:

1.8-3.5 mm. Colour, apart from the yellowish antennae, general appearance, setae, microsculpture on head and elytra as in *H. capillaricornis*. Pronotum, however, completely without microsculpture, antennae slenderer and abdomen very shiny with much less dense punctation and without any trace of microsculpture.

♂: tergite VII with weakly rounded, sternite VII with shallowly concave hind margins (Figs 9c-d); appendices of pleurites VIII with 1 seta; in contrast to the species of the *H. capillaricornis*-group without seta near the spiraculum of urite VIII (Fig. 9a); sternite VIII with extremely deep and broad emargination (Fig. 9b); posterior apex of sclerites IX rounded in lateral view (Fig. 9i); internal sac without large dark spines, internal row with ca. 30 semitransparent triangles (Fig. 11g).

♀: tergite and sternite VII transverse, the former with weakly rounded and the latter with nearly straight hind margins (Figs 9e-f); tergite VIII bluntly pointed, sternite VIII rounded posteriorly (Figs 9g-h).

DISTRIBUTION:

At present the species is only known from the north of Thailand and the surroundings of Bangkok.

BIONOMICS:

H. rougemonti was recorded at elevations of 900-1400 m. Several teneral specimens were collected in the beginning of November.

Habrocerus indicus spec. nov.

Figs 10, 11

HOLOTYPE: ♂, India; W. Bengal, Darjeeling Distr., Ghoom-Lopchu, 2000 m, 12.X.78, Besuchet & Löbl (MHNG).

PARATYPES: 1 ♀: same locality as holotype (MHNG); 3 ♂♂, 1 ♀: W. Bengal, Darjeeling Distr., Algarah-Labha, 1900 m, 11.X.78, Besuchet & Löbl (MHNG, Cass, Cwun), 1 ♀: India, Sikkim. Chungtang, 24.II.1952, T. Clay leg. (BMNH).

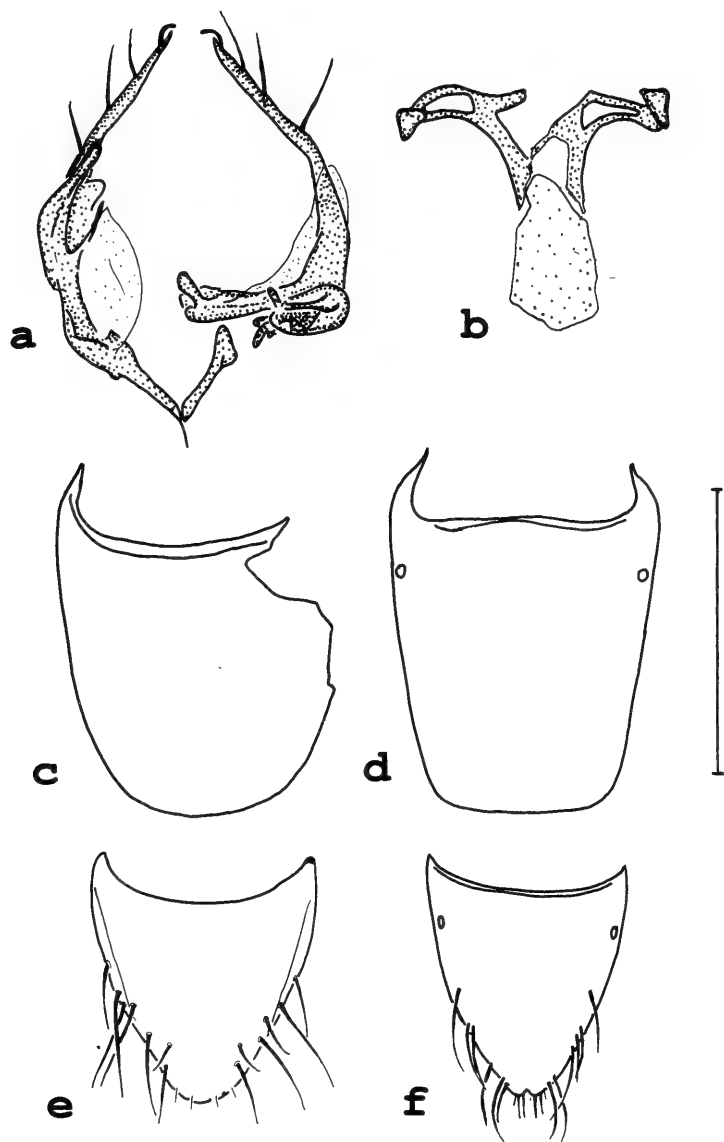


FIG. 15

Habrocerus costaricensis spec. nov.: pleurites and tergite of ♂ urite VIII (a); ♂ sternite VIII (b); ♂ sternite VII (c); ♂ tergite VII (d); ♀ sternite VIII (e); ♀ tergite VIII (f); setae and punctures omitted in c-d. Scale: 0.5 mm.

DESCRIPTION:

Size, body proportions, setae, punctation, microsculpture and colour as in *H. rougemonti*.

♂: tergite VII with weakly rounded, sternite VII with shallowly concave hind margins (as in *H. rougemonti*) (Figs 10c-d); appendices of pleurites VIII with 1 seta, shape of pleurites slightly different from that in *H. rougemonti*; without seta near the spiraculum of urite VIII (Fig. 10a); sternite VIII with deep V-shaped emargination, central part of sternite narrower than in *H. rougemonti* (Fig. 10b); posterior apex of sclerites IX pointed in lateral view (Fig. 10i); internal sac without large dark spines, internal row with ca. 80 semitransparent triangles (Fig. 11h).

♀: tergite and sternite VII transverse, the former with weakly rounded and the latter with nearly straight hind margins (Figs 10e-f); tergite and sternite VIII bluntly pointed posteriorly (Figs 10g-h).

DISTRIBUTION:

H. indicus is only known from the Himalayan regions in the north of India.

BIONOMICS:

Unknown.

III. The *Habrocerus schwarzi* species group***Habrocerus schwarzi* Horn**

Figs 13, 18

Habrocerus schwarzi Horn, 1877, *Trans. Amer. Ent. Soc.* 6: 124.

LECTOTYPE: ♀, designated here; labels: Mic, Paratype, 3146, G.H. Horn collection, Lectotypus *Habrocerus schwarzi* Horn 1877, desig. Assing & Wunderle 1992 (MCZ).

PARALECTOTYPE: ♀, labels: Mic, Paratype, 3146, G.H. Horn Collection (MCZ).

5 old specimens from the MCZ (G.H. Horn collection and LeConte collection) were examined. Although one of them was labeled 'type' and two further specimens were labeled 'paratype' there remained considerable doubt as to the exact identity of the holotype. Therefore, we chose to designate a lectotype from the Horn collection.

FURTHER MATERIAL STUDIED:

165 specimens from the BRI (157) and FMNH (8).

DESCRIPTION:

2.5-3.0 mm. Colour variable, usually with head, pronotum, antennae and anterior parts of tergites light to dark brown, elytra and hind margins of tergites yellowish to yellowish brown and the legs yellow.

Head somewhat shining with fine transverse microsculpture; antennal segments shorter than in *H. capillaricornis*, segment 3 distinctly shorter 4, segments 4-10 subequal in length. Pronotum 1.4-1.5x wider than long and with transverse microsculpture on whole surface. Anterior and lateral setae closer to margin, antero-lateral seta distinctly closer to anterior angle than in *H. capillaricornis*.

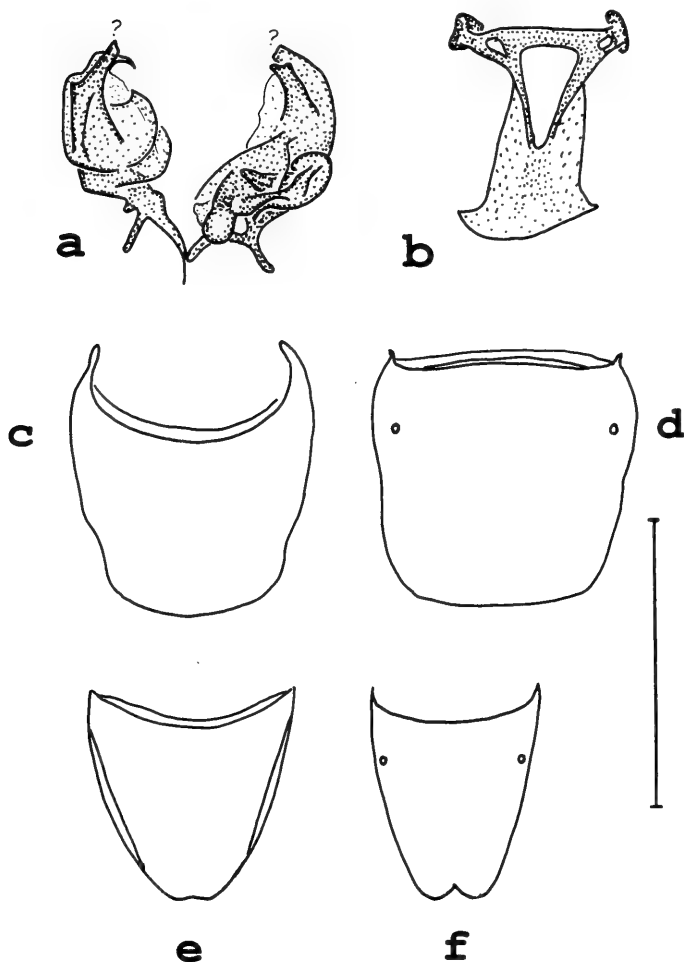


FIG. 16

Habrocerus tichomirovae (Filatova): pleurites and tergite of ♂ urite VIII, partly damaged (a); ♂ sternite VIII (b); ♂ sternite VII (c); ♂ tergite VII (d); ♀ sternite VIII (e); ♀ tergite VIII (f); setae and punctures omitted in c-f. Scale: 0.5 mm.

Elytra 1.7-1.8x wider than long (at suture), about as long as pronotum, with transverse microsculpture and sparse micropunctuation.

Tarsi of middle and hind legs shorter than in *H. capillaricornis*.

Abdomen with subdued shine due to short yellowish pubescence and fine dense microsculpture; number of setae on hind margins of tergites increasing caudally.

♂: tergite and sternite VII with often slightly asymmetrical, almost straight to weakly rounded hind margins (Figs 13c-d); sclerites of urites VIII and IX arranged asymmetrically (Figs 13a-b, g), a typical character shared by all the species of the *H. schwarzi* species group; appendices of pleurites VIII with 6-7 setae (Fig. 13a); sternite VIII without emargination, laterally with two asymmetric processes, anterior dilatation with lateral angles (Fig. 13b); internal sac with two rows of weakly sclerotized, roughly triangular structures (Fig. 18a).

♀: tergite VIII with ± deep U-shaped, relatively broad emargination (Fig. 13f), sternite VIII rounded with shallow central concavity posteriorly (Fig. 13e).

DISTRIBUTION:

Apart from one record in Alberta (George Lake, 11 specimens) all the material examined was collected in the northeast of North America, especially in Canada (Manitoba, Ontario, Quebec; altogether 134 specimens); only 20 specimens were from the U.S. (Massachusetts, Vermont, New Hampshire, New York, Wisconsin, Minnesota, Tennessee and Ohio). MOORE & LEGNER (1979) report the species for Michigan.

BIONOMICS:

According to the collection data on the labels of the specimens examined *H. schwarzi* appears to have a preference for old or dead fungi. It has also been found on moose dung, dead grouse and in leaf litter (one record each). All of the specimens were collected during the period from June through November, with a maximum in August. Immature adults were taken on August 5 and on September 15 (1 specimen each).

Habrocerus tropicus Wendeler, 1956

Figs 14, 18

Habrocerus tropicus Wendeler, 1956, *Dusenía* 7: 264f.

HOLOTYPE: ♀, Brasilien, Nova Teutonia, 27°11' B, 52°23' L, 300-500 m, Fritz Plaumann, Holotypus, *Habrocerus tropicus* n. sp., Wendeler det. (MHB).

PARATYPES: 1 ♂: same data as holotype (MHB); 1 ♀: Brasilien, Nova Teutonia, Fritz Plaumann coll. (MHB).

FURTHER MATERIAL STUDIED:

4 ♂♂, 6 ♀♀: Brazil, Nova Teutonia, 3-500 m, 27°11' B, 52°23' L, 1960-1972, F. Plaumann leg. (BRI); 1 ♂; 4 ♀♀: Brazil, Chapeco, 27°07' B, 52°36' L, 1960, F. Plaumann leg. (BRI); 5 ♀♀: Brazil, Sinimbu, 29°30', 52°30', 1960, Plaumann leg. (BRI); 1 ♀: Brazil, 18 km NE Oriximina, 1969, J.M. & B.A. Campbell leg. (BRI); 1 ♀: Brazil-Parana, Guarapuava, H. Schneider leg. (BRI); 1 ♀: Brazil, Nova Teutonia, F. Plaumann leg. (NHMV); 9 ♂♂, 28 ♀♀: Brazil, Nova Teutonia, 3-500 m, 27°11' B, 52°23' L, 1938, 1953-54, F. Plaumann leg. (FMNH); 6 ♂♂, 4 ♀♀: Brazil, Nova Teutonia (FMNH).

DESCRIPTION:

Size, body proportions, setae and microsculpture as in *H. schwarzi*; however, clearly darker in colour, in mature specimens usually whole body dark brown to

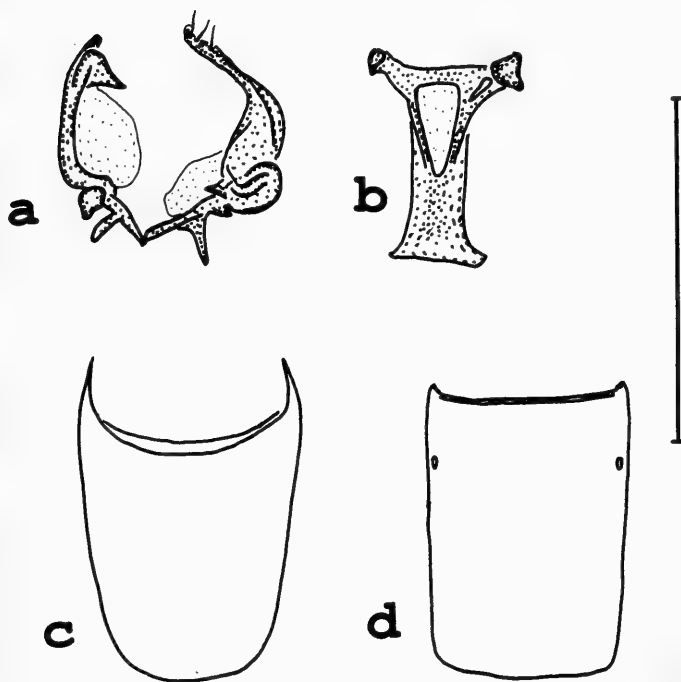


FIG. 17

Habrocerus schillhammeri spec. nov.: pleurites (partly damaged) and tergite of ♂ urite VIII (a); ♂ sternite VIII (b); ♂ sternite VII (c); ♂ tergite VII (d); setae and punctures omitted in c-d. Scale: 0.5 mm.

almost black with only the narrow hind margins of the tergites, and often the elytra, the legs, the antennae and the tip of the abdomen lighter.

♂: tergite VII with straight (Fig. 14d), sternite VII with rounded margin (Fig. 14c); sclerites of urites VIII and IX asymmetrical (Figs 14a-b; appendices of pleurites VIII with 5 setae, the subapical seta strongly bent (Fig. 14a); shape of sternite VIII similar to that in *H. schwarzi* (Fig. 14b); internal sac very long containing a large number of small sclerotized granula apically, but without rows of triangular structures (Fig. 18c).

♀: tergite VIII with deep and narrow, U-shaped emargination (Fig. 14f), the corresponding sternite rounded posteriorly (Fig. 14e).

DISTRIBUTION:

With the exception of 1 ♀ (Oriximina, North Brazil) all the specimens were collected in the southernmost part of Brazil (Santa Catarina, Rio Grande do Sul), south of Sao Paulo.

BIONOMICS:

The specimens examined were collected at elevations of 300-600 m from March through May and from July through December.

Habrocerus costaricensis spec. nov.

Fig. 15

TYPES: Holotype ♂, Costa Rica, Sa. Isidro ek Cor. (?), 3.VIII.39, A. Bierig Collection (FMNH). PARATYPES: 3 ♀♀: Costa Rica, Carpintera, 5.XI.39; 2 ♀♀: Costa Rica, Carpintera, 6.VIII.39; 1 ♀: Costa Rica, Carpintera, 6.VIII.41; 1 ♀: Carpintera, VIII.43; 1 ♀: Costa Rica, Sa. Isidro ek Cor. (?), 3.VIII.39; 1 ♀: Costa Rica, Tres Rios, 1.IX.40 (FMNH, Cass, Cwn).

DESCRIPTION:

Size, body proportions, setae and microsculpture as in *H. schwarzi*; colour darker, body brown to pitchy brown (often similar to *H. tropicus*) with the elytra, the posterior margins of the tergites and especially the tip of the abdomen usually somewhat lighter; legs and antennae light brown to brown.

♂: tergite VII with straight, sternite VII with rounded hind margin (Figs 15c-d); sclerites of urites VIII and IX arranged asymmetrically (Figs 15a-b); appendices of pleurites VIII with 4 setae, the subapical seta strongly bent (Fig. 15a); posterior lateral processes of sternite VIII long and asymmetrical (Fig. 15b).

♀: tergite VIII strongly converging posteriorly with very small emargination (Fig. 15f); hind margin of sternite VIII rounded (Fig. 15e).

DISTRIBUTION:

So far only known from Costa Rica.

BIONOMICS:

Apart from the data indicated above, the bionomics of *H. costaricensis* remain unknown.

Habrocerus tichomirovae (Filatova, 1981), comb. nov.

Fig. 16

Nomimocerus tichomirovae Filatova, 1981, *Rev. Ent. URSS* 60: 120f. figs.

HOLOTYPE ♂, Primorskij kraj, pos. Barabash-Levada, pojma r. Komissarovki pod, 24.VII.1978, Filatova (ZIAWP).

PARATYPES examined: 2 ♀♀, Primorskij kraj, Sichote-Alinskij Zapovednik, pod solomoj, 24.VIII.1978, Filatova (ZIAWP).

FURTHER MATERIAL STUDIED: 1 ♀, Russia, Khabarovsk Terr., Bikib Distr., 9 km SSE Boitsovo (FMNH).

DESCRIPTION:

Size, body proportions, microsculpture, punctation, arrangement of setae as in *H. schwarzi*. Head, pronotum, antennae, maxillary palpi and abdomen, except for the

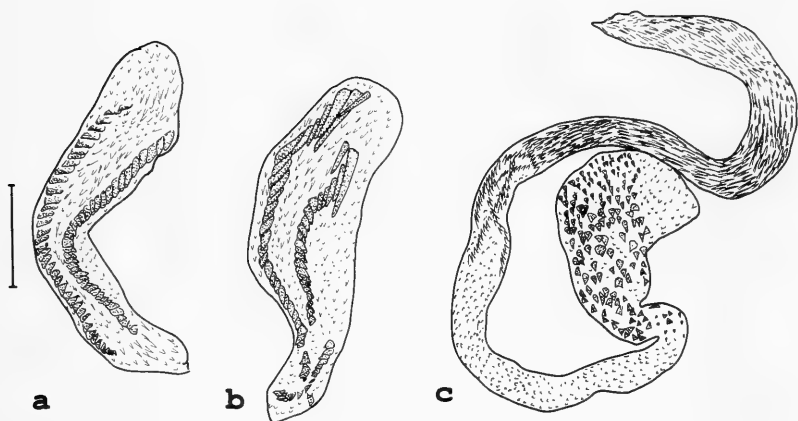


FIG. 18

The *Habrocerus schwarzi*-group: Internal sacs of *H. schwarzi* (a), *H. tichomirovae* (b) and *H. tropicus* (c). Scale: 0.25 mm.

hind margins of the tergites, brown to blackish brown; elytra light brown; legs yellowish brown.

♂: tergite VII almost straight posteriorly, sternite VII with sinuate sides and slightly rounded hind margin (Figs 16c-d); sclerites of urite VIII as in Figs 16a-b (appendices missing in holotype); internal sac with two rows of weakly sclerotized structures, most of which are of roughly triangular shape, whereas the apical ones are distinctly elongate (Fig. 18b).

♀: tergite VIII with angular, sternite VIII with variable, very weak to angular emargination posteriorly (Figs 16e-f).

Remarks: Since part of the genital armature of the only available ♂ (holotype) was missing, a description of the appendices and the number and shape of the setae, an important diagnostic character in the *H. schwarzi* species group, is not possible at present. However, as differences in the contents of internal sac as well as in the shapes of the ♀ tergite and sternite VIII can be observed, we think it best to treat *H. tichomirovae* as a valid species distinct from *H. schwarzi*, until further material of the former is available.

DISTRIBUTION:

H. tichomirovae is only known from Primorskiy kray, and Khabarovskiy kray, Russian Far East.

BIONOMICS:

The holotype and the paratypes were found under hay and straw, respectively. The ♀ from Khabarovsk Terr. was collected from "dead wood and litter in basal tree hole of small tree on hilltop".

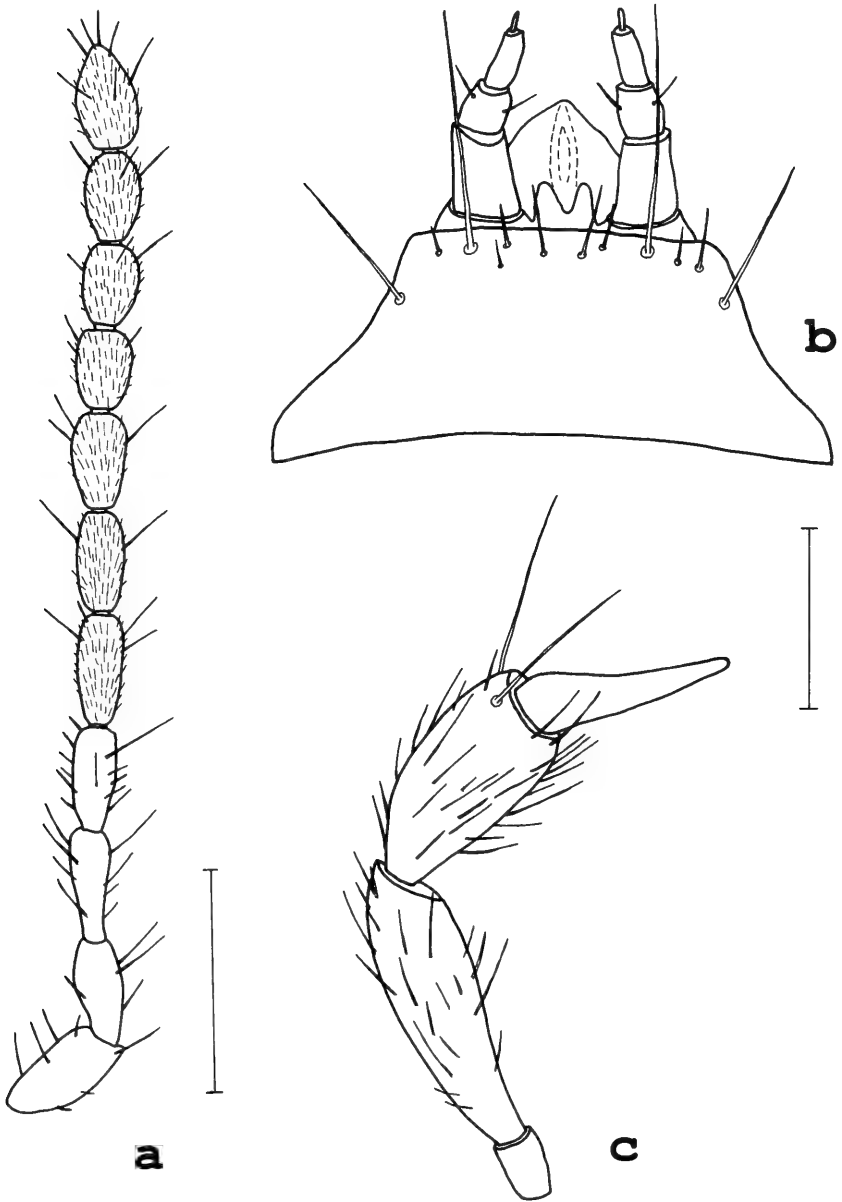


FIG. 19

Nomimocerus longispinosus spec. nov.: antenna (a); labium (b); maxillary palpus (c). Scale: 0.25 (a); 0.1 mm (b-c).

Habrocerus schillhammeri spec. nov.

Fig. 17

HOLOTYPE: ♂, N-Sumatra, 18.II., D. Toba s-Prapat, Lumbah Julu, Indonesia 1990, leg. Schillhammer (NHMW).

DESCRIPTION:

Length of holotype: 2.0 mm. Easily distinguished from all other known species of *Habrocerus* by size alone. Colour of head black; pronotum pitchy brown; elytra only in part slightly lighter; antennae brown, legs light brown; abdomen dark brown with hind margins of tergites and tergite VII lighter in colour.

Head, pronotum and elytra with fine transverse microsculpture; pronotal, elytral and abdominal setae relatively long and stout, their insertions as in *H. schwarzi*. Elytral suture slightly (0.9x) shorter than pronotum.

Hind tibiae relatively longer than in *H. schwarzi*.

Abdomen with pubescence less dense, but longer than in *H. schwarzi*.

♂: tergite VII with almost parallel sides and with straight hind margin (Fig. 17d), the corresponding sternite broadly rounded posteriorly (Fig. 17c); sclerites of urite VIII asymmetrical; appendices of pleurites VIII with 3 (?) setae (Fig. 17a); shape of sternite VIII similar to that in *H. schwarzi* (Fig. 17b).

Remarks: Since relevant parts of the internal sac were damaged, it was not possible to illustrate its contents.

DISTRIBUTION:

So far only known from the type locality in Sumatra.

BIONOMICS: Unknown.

Habrocerus magnus Leconte, non *Habrocerus*

Habrocerus magnus Leconte, 1878, Proc. Amer. Philos. Soc. 57: 598.

An examination of the type (♂: USA, Isle Royal, 14.7LS, 29, Type 6510, H. magnus, J.L. LeConte Collection) in MCZ and further specimens (1 in MCZ and 5 in FMNH) revealed that this species neither belongs to the genus *Habrocerus* nor the subfamily Habrocerinae, but apparently to some tachyporine genus unknown to us. It lacks several characteristics of *Habrocerus* and Habrocerinae, respectively, the chief amongst them being the filiform antennae, the absence of an aedeagus and the typical abdominal modifications in the males. LECONTE himself seems to have been uncertain as to the generic identity of this species, which can be concluded from the question mark in his description.

H. magnus is here excluded from the genus *Habrocerus*.

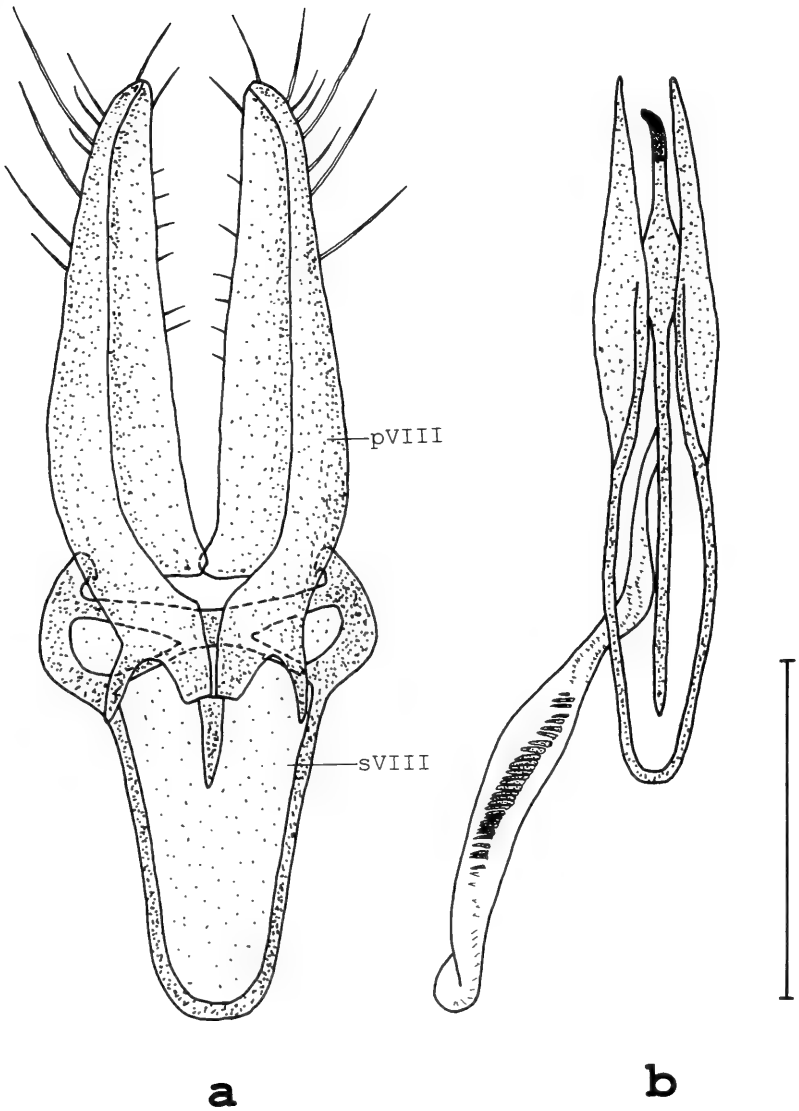


FIG. 20

Nomimocerus longispinosus spec. nov.: ♂ urite VIII in dorsal view (a); ♂ urite IX and internal sac (b); pVIII = pleurite VIII, sVIII = sternite VIII. Scale: 0.5 mm.

THE GENUS **Nomimocerus** COIFFAIT & SAIZ, 1965

COIFFAIT & SAIZ (1965) based their description of *Nomimocerus* on the type species *N. marginicollis* (Solier) from Chile, originally described as *Tachyporus marginicollis*. Since then only one further *Nomimocerus* has been described, *N. tichomirovae* Filatova, which, however, is here transferred to *Habrocerus* (see above).

MORPHOLOGY

Nomimocerus is identified as a habrocerine genus on the basis of the following characters: the absence of an aedeagus, the modifications of the last abdominal segments in the males (see below) and the flat triangular shape of the hind coxae. In addition, it very much resembles *Habrocerus* in general appearance, body size, sculpture and colour. Unlike *Habrocerus*, however, *Nomimocerus* possesses non-filiform antennae (Fig. 19a) and 4-segmented labial palps (Fig. 19b). Furthermore, the shape of the modified male urites, particularly the appendices of pleurites VIII, a character also visible in dried specimens, is clearly different (Fig. 20).

In *Nomimocerus* males tergite VII carries a membranous appendage posteriorly. The hind margin of sternite VII is concave or emarginate. The species differ with regard to this character, which is, however, subject to some intraspecific variability and thus not very reliable. The male genital armature is characterized by two somewhat massive pleurites VIII, which together are of scoop-like appearance, dorsally connected and ventrally linked to sternite VIII. The latter is U-shaped anteriorly and forms a wide X posteriorly (Fig. 20a). Segment IX, too, is highly modified and principally of similar construction as in *Habrocerus*. It consists of two anteriorly connected lateral lobes and a rode-like structure in the centre, the latter apically bent like a hook (Fig. 20b). The internal sac, which contains rows of spines of specific shapes and sizes, represents the most important and reliable differential character for the identification of the species of *Nomimocerus*.

In the females the hind margins of tergite and sternite VIII are rounded (Fig. 21b, c). As in *Habrocerus*, urite IX carries two stylus-shaped processes, the tips of which are visible in normal position (Fig. 21a).

Further morphological details are presented by COIFFAIT & SAIZ (1965). It should be noted, however, that their illustrations contain several errors: Figs 2a-c depict the male urite VIII (not the aedeagus, as indicated in the legend), Fig. 2e shows the tergite VIII of a female *Habrocerus* [!] (not the fifth sternite of a male *Nomimocerus*) and Fig. 2f represents the female urite IX of *Habrocerus* [!] (not the male genital segment of *Nomimocerus*).

THE SPECIES OF **Nomimocerus**

An examination of the *Nomimocerus* material of several museum collections including the lectotype of *N. marginicollis* showed that at present 4 species can be

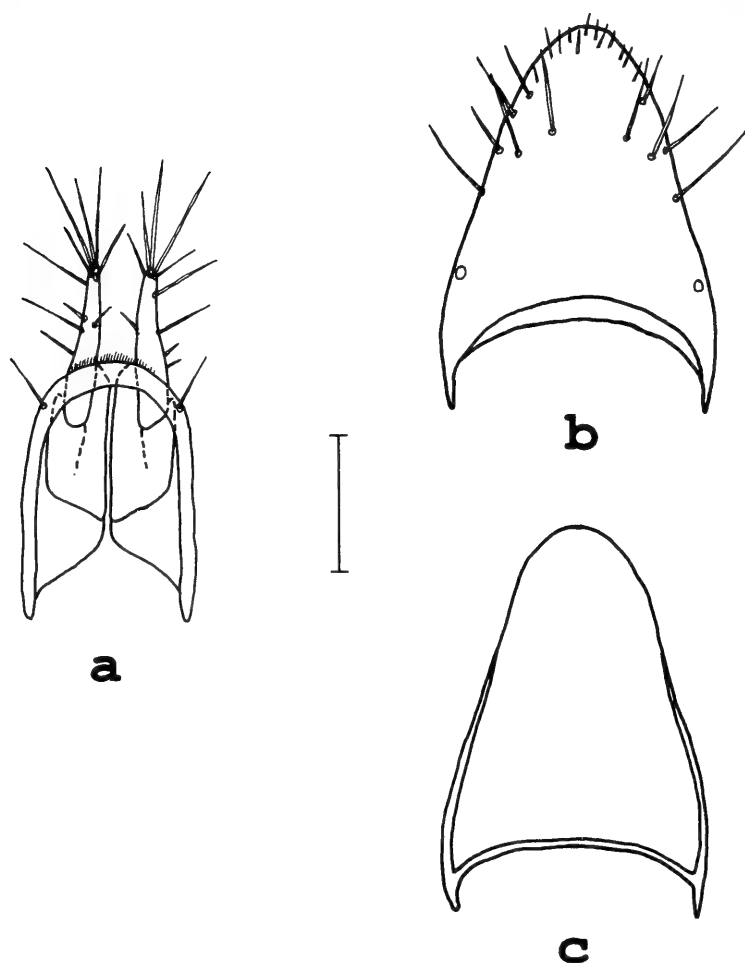


FIG. 21

Nomimocerus longispinosus spec. nov.: ♀ urite IX (a); ♀ tergite VIII (b); ♀ sternite VIII (c); setae and punctures omitted in c. Scale: 0.25 mm.

distinguished: *N. marginicollis*, *N. longispinosus* sp. n., *N. peckorum* sp. n. and *N. parvispinosus* sp. n. Since material of *Nomimocerus* appears to be rather scarce in the major collections and since three of the species are presently known only from one locality each, further species are very likely to be discovered in the future. The distribution of *Nomimocerus* seems to be restricted to the south of South America. The only species described from a different region (*N. tichomirovae*) turned out to be a *Habrocerus*.

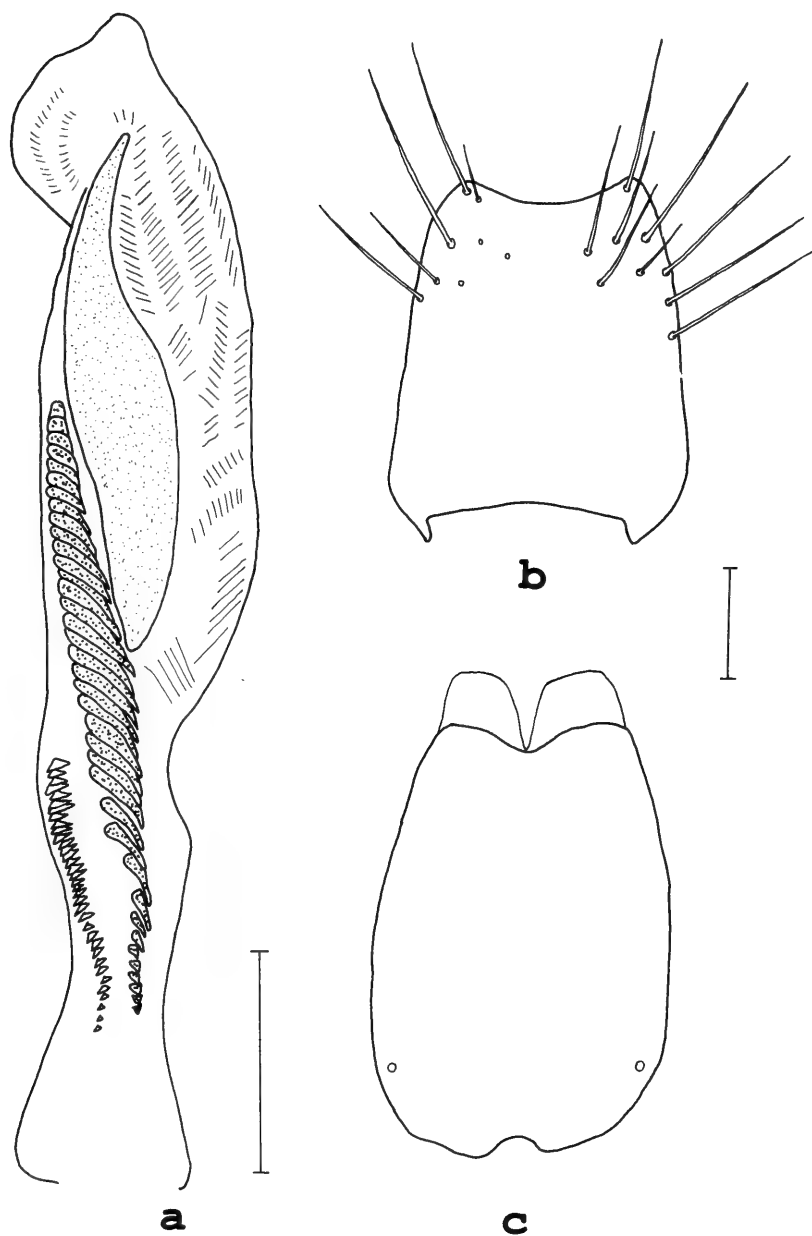


FIG. 22

Nomimocerus marginicollis (Solier) ♂: internal sac (a); sternite VII (b); tergite VII (c); setae and punctures omitted in c. Scale: 0.25 mm.

Regarding their external morphology the species of *Nomimocerus* are highly similar. Apart from the somewhat variable shape of the hind margin of the male sternite VIII, no consistent differences were found, although a variety of characters and measurements were considered. Surprisingly, the same even applies to the complex structure of the male genital armature. The arrangement, size and shape of spines and further sclerotized structures in the internal sac were found to be the only safe and reliable differential characters, a situation similar to that in other staphylinid taxa (e.g. Xantholininae, Aleocharinae, etc.). In order to evaluate the internal sac properly it is necessary to squeeze it lightly and to examine it under the microscope at magnifications of 200–400x.

Since the four species treated below are highly similar regarding their external morphology we consider it sufficient to describe only *N. marginicollis* in full detail. The descriptions of the following species will then focus on differential characters.

***Nomimocerus marginicollis* (Solier, 1849)**

Fig. 22

Tachyporus marginicollis Solier, 1849, in: Gay, *Hist. Chile* 4: 343.

Tachyporus marginicollis var. *rufescens* Solier, 1849, in: Gay, *Hist. Chile* 4: 343.

Habrocerus marginicollis; KRAATZ, 1859, *Berl. Ent. Zeit.* 3: 10, 13.

Habrocerus marginicollis; FAIRMAIRE & GERMAIN, 1861, *Annal. Soc. entomol.* Fr. 1: 425.

Habrocerus marginicollis; FAUVEL, 1864, *Annal. Soc. entomol.* Fr. 4: 124.

Habrocerus marginicollis; FAUVEL, 1866, *Bull. Soc. Sinn. Norm.* 10: 331f.

Nomimocerus marginicollis; COIFFAIT & SAIZ, 1965, *Bull. Soc. Hist. Nat. Toulouse* 100: 218 ff. figs.

LECTOTYPE: ♀; labels: Puerto Montt, Chili, *marginicollis* Sol., *Habrocerus*, coll. et det. A. Fauvel (IRSNB; Nr. 17479).

FURTHER MATERIAL STUDIED: 1 ♂, same data as lectotype and labelled 'Ex-Typis' (IRSNB).

DESCRIPTION:

3.5–4.0 mm. Measurements of pronotum and elytra of lectotype: length (PL) and width (PW) of pronotum 0.71 mm and 1.07 mm, respectively; length of elytral suture (EL) 0.83 mm. Head, pronotum, elytra and legs light to dark brown; abdomen dark brown to blackish brown with the hind margins of the tergites somewhat lighter; antennae yellow to yellowish brown, basal segments a little lighter in colour than apical half of antenna.

Head with large eyes reaching hind margin, surface somewhat shining despite clear transverse microsculpture. Antenna with first segment longer and wider than segment 2; segments 3–10 gradually decreasing in length and increasing in width, the distinctly elongate segments 3–6 ca. 3x and the suboval segments 9–10 ca. 1.5 x longer than wide; segments 5–11 with inconspicuous but very dense pubescence (cf. Fig. 19a).

Pronotum ca. 1.5x wider than long (see measurements) with arcuate sides and rounded anterior and posterior angles; its surface somewhat shining, but with distinct transverse microsculpture; altogether with 12 long setae; 4 equally spaced setae near

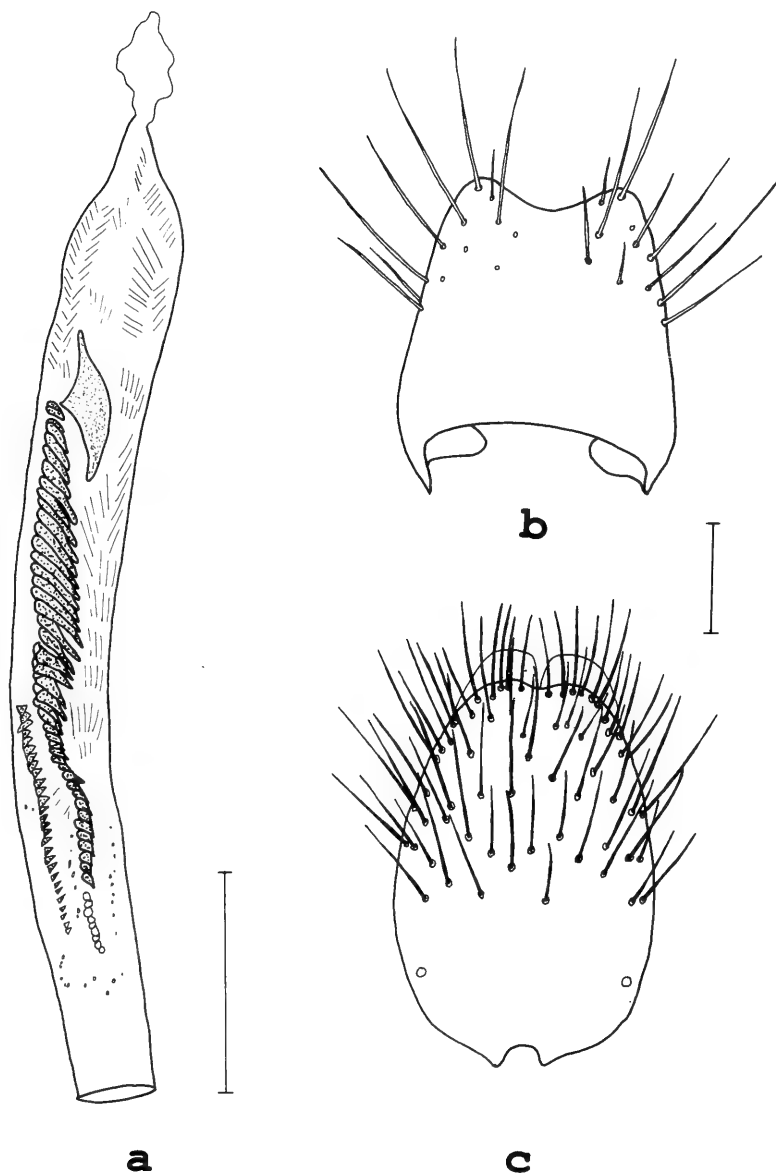


FIG. 23

Nomimocerus longispinosus spec. nov. ♂: internal sac (a); sternite VII (b); tergite VII (c).
Scale: 0.25 mm.

front margin, 2 in the front corners, 2 central and 2 posterior setae near lateral margin and 2 at basal margin.

Elytra, along suture, slightly longer than pronotum; microsculpture similar to that of pronotum; each with one humeral and two lateral punctures bearing long setae and with one short bristle near the sutural angle.

Legs moderately long; front coxae approximately as long and as wide as front femora, the latter distinctly wider than mid- and hind femora; hind tarsi reaching $2/3$ of length of hind tibiae, the first tarsal segment distinctly elongate, almost as long as segments 2-4 together.

Abdomen with surface of tergites mostly smooth between punctures, but subdued shine due to dense pubescence; hind margins of tergites with variable number of long setae: tergite III: 4-6, IV: 10-12, V: 12-14, VI: 10-14.

♂: hind margin of tergite VII slightly emarginate with membranous appendage split in the middle; sternite VII with hind margin broadly concave (Figs 22 b-c).

Scoop-like lobes of urite VIII larger than in the following species (cf. Fig. 20a). Internal sac with a large sclerotized piece, a row of about 30 relatively slender and long spines and a further row of minute spines (Fig. 22a).

♀: tergite and sternite VIII rounded apically (cf. Fig. 21a-c).

Remarks: FAUVEL (1864; 1866) and KRAATZ (1859) state that the type of *Nomimocerus rufescens* (Solier) is an immature specimen of *N. marginicollis*. Since half of the type is missing (KRAATZ 1859) and, consequently, it is impossible to confirm or disprove their opinion, we follow these authors and regard *N. rufescens* as a synonym of *N. marginicollis*.

DISTRIBUTION:

According to COIFFAIT & SAIZ (1965) the species is known from the province of Valdivia, from Chiloe and Puerto Montt.

However, since *N. marginicollis* is the only species known before and since we have been unable to examine specimens from the first two locations, Puerto Montt must, at present, be considered the only safe record of the species.

BIONOMICS: Unknown.

Nomimocerus longispinosus spec. nov.

Figs 19, 20, 21, 23

HOLOTYPE: ♂, labels: Chile: Aysen Prov., 34 km W Pto. Aysen, San Sebastian, 150 m, 24.I.1985, cliffbase, mixed forest bamboo litter, S. & J. Peck, berlese (FMNH).

PARATYPES: 28 ♂♂, 20 ♀♀: same data as holotype; 8 ♂♂, 9 ♀♀: Chile, Aysen Prov., 33 km E Pto. Aysen, Rio Simpson N.P., 70 m, 26.I.1985, forest sifted leaf and stick litter, S. & J. Peck (FMNH, Cass, Cwun).

DESCRIPTION:

3.5-4.0 mm. Measurements of pronotum and elytra: PL: 0.63-0.70 mm; PW: 0.9-1.05 mm; EL: 0.62-0.72 mm.

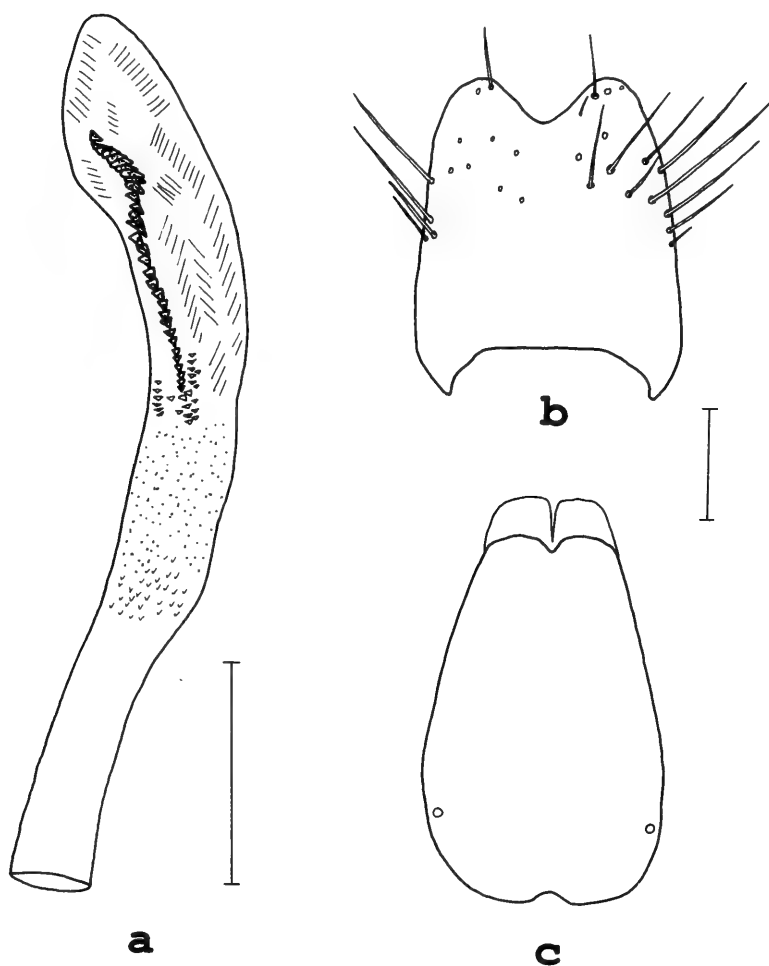


FIG. 24

Nomimocerus parvispinosus spec. nov. ♂: internal sac (a); sternite VII (b); tergite VII (c); setae and punctures omitted in c. Scale: 0.25 mm.

Colour variable; head, pronotum and elytra reddish brown to dark brown with the head often darker and the pronotum, especially the sides, usually lighter; abdomen blackish brown with the hind margins of the tergites lighter in colour; colour of appendages as in *N. marginicollis*.

In external morphology (proportions, microsculpture, punctures) highly similar to *N. marginicollis*; abdomen slightly less shining due to superficial microsculpture between punctures.

Hind wings reduced, only slightly longer than elytra, in all the specimens examined.

♂: tergite VII smaller than in *N. marginicollis*, its hind margin with weak concave emargination in the middle (Fig. 23c); emargination of posterior margin of sternite VII wide and usually deeper than in *N. marginicollis*, but not as deep as in the following species (Fig. 23b); internal sac with a rather small sclerotized piece visible in transparent light, a characteristic row of partly long spines (name!) and a short row of minute spines (Fig. 23a).

♀: last abdominal segments as in Figs 21a-c.

DISTRIBUTION:

All the specimens studied were collected near Puerto Aysen (Aisen) in the south of Chile (ca. 45° southern latitude).

BIONOMICS:

The type material was extracted or sifted from leaf and stick litter and bamboo litter in mixed forests at lower elevations (70-150 m). A considerable proportion of the beetles collected in January was immature. All 66 specimens were brachypterous and thus incapable of flight.

Nomimocerus parvispinosus spec. nov.

Fig. 24

HOLOTYPE: ♂; labels: S. Arg. Rio Negro, El Bolson, Topal, Nr. 543, 8.IX.61, *marginicollis* Solier, ex coll. Scheerpeltz (NHMW).

PARATYPES: 5 ♂♂, 5 ♀♀: same locality as holotype, dates of collection 14.VI.61 (4 ♂♂, 1 ♀), 6.XI.61 (1 ♂), 13.V.61 (1 ♀), 8.IX.61 (1 ♀), 22.IX.61 (2 ♀♀), 15.IX.61 (1 ♀); 1 ♂: Chile, Umg. Santiago, Sterc. Bovin., Kuschel (NHMW, Cass, Cwun).

DESCRIPTION:

3.5-4.0 mm. Measurements of pronotum and elytra: PL: 0.63-0.72 mm; PW: 0.9-1.1 mm; EL: 0.65-0.85 mm.

Colour of head, pronotum and elytra brown to dark brown with the head often darker and the sides of the pronotum usually yellowish brown; abdomen blackish brown with the hind margins of the tergites lighter in colour; colour of appendages as in *N. marginicollis*.

External morphology (proportions, microsculpture, punctures) highly similar to *N. marginicollis*; abdomen slightly less shining due to superficial microsculpture between punctures. Hind wing development dimorphic, elytra somewhat longer in macropterous specimens (distinctly longer than pronotum) than in those with reduced alae (about equal in length to pronotum).

♂: shape of tergite VII as in *N. marginicollis*, but smaller (Fig. 24c); emargination of hind margin of sternite VII usually relatively deep and roughly triangular (Fig. 24b), rarely shallow and almost concave; internal sac smaller than in *N.*

marginicollis, with one row of 30-40 small spines (name!) and without distinct sclerotized piece (Fig. 24a).

♀: last segments of abdomen as in *N. longispinosus*.

DISTRIBUTION:

N. parvispinosus is only known from the type locality in Argentina and the surroundings of Santiago de Chile.

BIONOMICS: Unknown.

Nomimocerus peckorum spec. nov.

Fig. 25

HOLOTYPE: ♂; labels: Chile, Osorno Prov., Puyehue N.P. Anticura, Repucura Tr., 500 m, 6.II.1985, forest litter, S. & J. Peck, berlese (FMNH).

PARATYPES: 2 ♀♀: same data as holotype; 1 ♀: Chile: Osorno Prov., Puyehue Nat. Pd., Antillarca Rd., 500-1000 m, 18.-20.XII.1984, S. & J. Peck, carnetting; 1 ♂: Chile: Osorno Prov., Puyehue Nat. Pk., Antillanca Rd., 470 m, 20.-24.XII.1982, Valdivian rainforest, leaf & log litter, A. Newton & M. Thayer; 1 ♀: Chile: Osorno Prov., Puyehue Nat. Pk., Antillanca Rd., 690 m, 20.-24.XII.1982, Valdivian rainforest, leaf & log litter, A. Newton & M. Thayer; 1 ♂: Chile, Osorno Prov., Puyehue Nat. Pk., Antillanca Rd., 845 m, leaf & log litter, 18.-24.XII.1982, A. Newton & M. Thayer; 1 ♂, 1 ♀: Chile, Llanquihue Prov., Salto Petrohue, V. Perez Nat. Pk., 150 m, 23.XII.1984, mixed forest litter, S. & J. Peck (FMNH, Cass, Cwun).

DESCRIPTION:

3.5-4.0 mm. Measurements of pronotum and elytra: PL: 0.63-0.70 mm; PW: 0.9-1.1 mm; EL: 0.61-0.73 mm.

Colour variable; head, pronotum and elytra reddish brown to dark brown with the head often darker and the sides of the pronotum lighter; abdomen blackish brown with the hind margins of the tergites lighter in colour; colour of appendages as in *N. marginicollis*.

In external morphology (proportions, microsculpture, punctures) highly similar to the other species; shine and microsculpture of abdomen as in *N. longispinosus* and *N. parvispinosus*.

Hind wings reduced, only slightly longer than elytra, in all the specimens included in the type series.

♂: tergite VII smaller than in *N. marginicollis*, its shape as in *N. longispinosus* (Fig. 25c); emargination of posterior margin of sternite VII triangular, deeper than in the other species (Fig. 25b); internal sac with a large sclerotized piece and a series of spines, part of which are characteristically shaped with a bulbous base and a slender apical process (Fig. 25a).

♀: last abdominal segments as in *N. longispinosus*.

DISTRIBUTION:

Presently the species is only known from the type locality and its surroundings south of Valdivia, Chile.

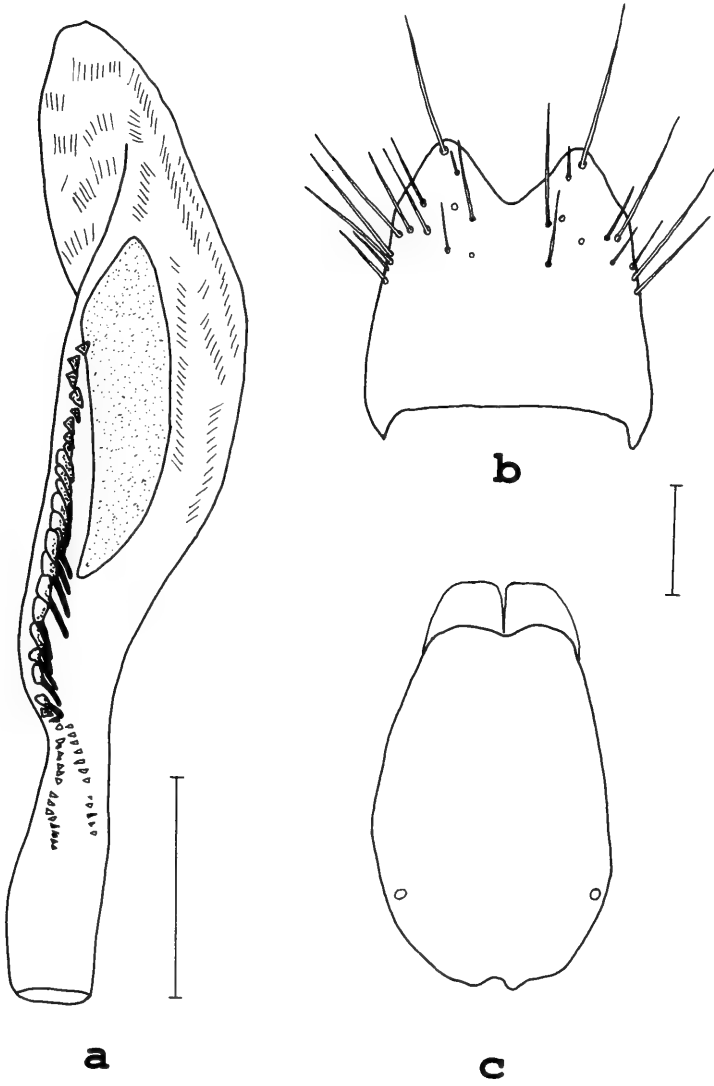


FIG. 25

Nomimocerus peckorum spec. nov. ♂: internal sac (a); sternite VII (b); tergite VII (c); setae and punctures omitted in c. Scale: 0.25 mm.

BIONOMICS:

The species was collected from leaf and log litter in Valdivian rainforest and in mixed forest at various elevations (150-850 m) in December. According to the labels some adult beetles were found together with larvae. All the specimens included in the type series were brachypterous and thus incapable of flight. However, on one of the locations indicated above a macropterous *Nomimocerus* ♀ was collected, which might belong to the same species, but was considerably larger and darker and had distinctly longer elytra.

KEY TO GENERA OF HABROCERINAE

1. Antenna filiform with segments 3-11 distinctly narrower than first two segments (Fig. 1a); labial palps 3-segmented.
♂: tergite VII with inconspicuous complete membranous appendage posteriorly, hind margin of sternite VII rounded, straight or, at the most, very shallowly concave, urite VIII with long spine-shaped appendices crossed in normal position (Fig. 2).
♀: hind margins of tergite and sternite VIII rounded, pointed or emarginate *Habrocerus* Erichson
- Antennal segments 3-11 subequal in width to first two segments or only slightly narrower; labial palps 4-segmented.
♂: tergite VII with conspicuous, deeply incised membranous appendage posteriorly, hind margin of sternite VII with broadly concave or triangular emargination, urite VIII with large appendices together forming scoop-like structure (usually visible at least in part in mounted specimens) (Fig. 20a).
♀: posterior margins of tergite and sternite VIII rounded (Figs 21a-c)
..... *Nomimocerus* Coiffait & Saiz

KEY TO SPECIES OF HABROCERUS

1. On average larger in size (3.0-4.5 mm); anterior lateral seta of pronotum clearly distant from anterior pronotal margin; pronotum with or without microsculpture.
♂: genital sclerites almost symmetrical; anterior margin of sternite VIII rounded, its posterior margin with emargination of various shapes (cf. Fig. 4b); appendices of pleurites VIII with at the most 2 long setae.
♀: posterior margins of tergite VIII bluntly to acutely pointed (cf. Figs 4g, 10g).
West Palearctic, Oriental region 2
- On average smaller in size (2.0-3.0 mm); anterior lateral seta of pronotum very close to anterior pronotal margin; microsculpture on pronotum always clearly visible.

♂: genital sclerites asymmetrical; anterior margin of sternite VIII almost straight and laterally with tooth-like processes, its posterior margin without central emargination (cf. Fig. 13b); appendices of pleurites VIII with 3 or more long setae.

♀: posterior margin of tergite VIII more or less emarginate. New World¹, East Palaearctic, Indo-Malayan region.

The *Habrocerus schwarzi* species group 9

2. Pubescence of abdomen dense, fine microsculpture on tergites sometimes weak, but always visible.

♂: urite VIII with seta near spiraculum (as in Fig. 4a); posterior part of sternite VIII with apices of lateral processes of more complex construction, small tooth-like processes at the sides of central emargination of hind margin almost always present (Fig. 4b); internal sac often with large dark spines (Figs 12a-d).

♀: Posterior margins of tergite and sternite VIII acutely pointed (as in Figs 4g-h).

West Palaearctic.

The *Habrocerus capillaricornis* species group 3

- Abdomen very shining, without microsculpture and with less dense pubescence.

♂: urite VIII without seta near spiraculum (Figs 9a, 10a); apices of latero-posterior processes of sternite VIII simple, central emargination of hind margin without tooth-like processes (Figs 9b, 10b); internal sac without large dark spines (Figs 11g-h).

♀: Posterior margins of tergite and sternite VIII rounded or bluntly pointed (Figs 9g-h, 10g-h).

Oriental region.

The *Habrocerus rougemonti* species group 8

3. Disc of pronotum usually without transverse microsculpture, which may, however, be present on the sides and near the hind margin.

♂: appendices of pleurites VIII with two long setae (as in Fig. 3a).

♀: posterior margin of sternite VII weakly concave (cf. Fig. 3f) 4

- Transversely striate microsculpture on disc of pronotum usually clearly visible.

♂: appendices of pleurites VIII with 1 long seta (cf. Fig. 4a).

♀: sternite VII straight or rounded posteriorly.

Species that can be identified with certainty only in the male sex 6

4. Colour of pronotum and elytra usually uniformly light to dark brown; shape of body more elongate, smaller (3.0-4.0 mm).

¹ Note that *H. capillaricornis* has become indigenous in North America only in this century and that it is here considered a West Palaearctic species.

- ♂: appendices of pleurite VIII weakly bent (Figs 3a, 6a); central emargination of posterior margin of sternite VIII with distinct tooth-like processes (Figs 3b, 6b).
- ♀: tergite VIII extremely pointed posteriorly (Figs 3g, 6g) 5
- Body usually bicoloured with the pronotum darker than the elytra; body of broader shape and larger size (3.5–4.5 mm).
- ♂: appendices of pleurite VIII distinctly curved (Fig. 8a); central emargination of posterior margin of sternite VIII without processes (Fig. 8b); internal sac with a row of large dark, extremely wide-based spines and a number of additional dark spines of various shapes (Fig. 11b).
- ♀: tergite VIII simply pointed posteriorly (Fig. 8g).
- Endemic to Canary Islands. *H. canariensis* sp. n.
5. ♂: central emargination of posterior margin of sternite VIII narrower with tooth-like processes subparallel (Fig. 3b); internal sac with a row of 6 large and dark, wide-based spines and ca. 8 additional small sclerotized structures of roughly triangular shape (Fig. 11a).
- ♀: tergite and sternite VIII less transverse, the latter with hind margin simply angled (Figs 3g–h).
- West Palaearctic, introduced in North and South America.
- *H. capillaricornis* (Grav.)
- ♂: central emargination of hind margin of sternite VIII broader with tooth-like processes slightly converging posteriorly (Fig. 6b); internal sac without large dark spines (Fig. 11f).
- ♀: tergite and sternite VIII more transverse, the latter with hind margin pointed in the middle (Fig. 6g–h). Endemic to Cyprus. *H. cyprensis* sp. n.
6. ♂: internal sac larger, containing a number of dark spines (Figs 11c, d). 7
- ♂: internal sac small, without dark spines (Fig. 11e).
- Southwest Europe. *H. ibericus* sp. n.
7. ♂: central emargination of posterior margin of sternite VIII with short and blunt, but distinct tooth-like processes (Fig. 4b); internal sac larger, with a row of ca. 11 large dark spines of elongate, roughly triangular shape (Fig. 11c).
- Balkan, Northeast Mediterranean, Southern Italy. *H. pisidicus* Korge
- ♂: central emargination of posterior margin of sternite VIII with very indistinct processes (Fig. 5b); internal sac smaller, containing 5–6 large dark elongate spines (Fig. 11d). East Mediterranean from East Anatolia to Israel. *H. simulans* sp. n.
8. ♂: hind margin of sternite VIII deeply and broadly emarginate, U-shaped (Fig. 9b). Sclerites of urite IX apically rounded in lateral view (Fig. 9i); internal sac containing a central row of ca. 30 weakly sclerotized, triangular structures (Fig. 11g).
- Thailand. *H. rougemonti* Pace
- ♂: hind margin of sternite VIII narrower and V-shaped (Fig. 10b); pleurites VIII of different shape (10a); sclerites of urite IX apically

pointed in lateral view (Fig. 10i); internal sac containing a central row of ca. 80 weakly sclerotized, triangular structures (Fig. 11g).

India (Darjeeling). *H. indicus* sp. n.

9. Larger species, 2.5-3.0 mm; tergites with rather dense pubescence.
New World, East Palaearctic. 10
- Very small species, 2 mm; tergites with less dense pubescence; pronotal and elytral setae rather long and stout.
♂: tergite VII with almost parallel sides and roughly straight hind margin (Fig. 17d); sclerites of urite VIII as in Figs 17a-b.
Sumatra. *H. schillhammeri* sp. n.
10. Colour of body lighter on average, brown to dark brown with the elytra often yellowish to reddish brown.
♂: appendices of pleurite VIII with 6-7 setae (number of setae in *H. tichomirovae* unknown!) (Fig. 13a).
North America, East Palaearctic. 11
- Body colour darker on average, dark brown to blackish brown with the elytra often somewhat lighter.
♂: appendices of pleurite VIII with less than 6 setae (Figs. 14a, 15a).
Central and South America. 12
11. ♂: internal sac with two rows of weakly sclerotized triangular structures of roughly the same size (Fig. 18a); tergite and sternite VII as in Figs 13c-d; appendices of pleurites VIII with 6-7 setae (Fig. 13a); sternite VIII and sclerites of urite IX as in Figs 13b, g.
♀: tergite VIII with deep rounded emargination posteriorly (Fig. 13f); sternite VIII as in Fig. 13e.
North America. *H. schwarzi* Horn
- ♂: internal sac with two rows of weakly sclerotized structures strongly increasing in size and length apically (Fig. 18b); number of setae on appendices of pleurites VIII unknown.
♀: hind margin of tergite VIII with angular emargination (Fig. 16f); sternite VIII as in Fig. 16e.
Russian Far East. *H. tichomirovae* (Filatova)
12. ♂: appendices of pleurites VIII with 5 setae (Fig. 14a); internal sac very long (Fig. 18c).
♀: tergite VIII with deep, U-shaped incision posteriorly (Fig. 14f).
South America. *H. tropicus* Wendeler
- ♂: appendices of pleurite VIII with 4 setae (Fig. 15a).
♀: tergite VIII with very small incision posteriorly (Fig. 15f).
Costa Rica. *H. costaricensis* sp. n.

KEY TO SPECIES OF NOMIMOCERUS

1. ♂: internal sac without distinct sclerotized piece and with a relatively short row of minute spines (Fig. 24a); emargination of hind margin of sternite VII usually roughly triangular (Fig. 24b).

- Argentina, Chile. *N. parvispinosus* sp. n.
- ♂: internal sac with distinct sclerotized piece and a relatively long row of — at least partly — elongate spines, sometimes with an additional short row of minute spines; emargination of hind margin of sternite VII triangular to shallowly concave. 2
2. ♂: central spines in internal sac of characteristic shape, with bulbous bases and elongate apices (Fig. 25a); emargination of hind margin of sternite VII triangular (Fig. 25b).
- Chile. *N. peckorum* sp. n.
- ♂: spines in internal sac of different shapes; hind margin of sternite VII shallowly concave. 3
3. ♂: sclerites of urites VII-IX and internal sac larger than in the other species, concavity of hind margin of sternite VII very shallow (Fig. 22b); internal sac with long sclerotized piece (Fig. 22a).
- Chile. *N. marginicollis* (Solier)
- ♂: sclerites of urites VII-IX and internal sac smaller, concavity of hind margin of sternite VII deeper; sclerotized piece in internal sac short and of different shape (Fig. 23a).
- Chile *N. longispinosus* sp. n.

RÉSUMÉ: RÉVISION DES ESPÈCES DE LA SOUS-FAMILLE HABROCERINAE (COLEOPTERA: STAPHYLINIDAE) DU MONDE.

Actuellement la sous-famille Habrocerinae comprend deux genres, *Habrocerus* Erichson et *Nomimocerus* Coiffait & Saiz. Une révision à l'échelle mondiale du genre *Habrocerus* Erichson a révélé dans l'ensemble 13 espèces valides. 7 nouvelles espèces sont décrites: *H. ibericus* sp. n. du sud-ouest de l'Europe, *H. simulans* sp. n. de la région est de la Méditerranée, *H. cyprensis* sp. n. de Chypre, *H. canariensis* sp. n. des îles Canaries, *H. indicus* sp. n. d'Inde, *H. costaricensis* sp. n. de Costa Rica et *H. schillhammeri* sp. n. de Sumatra. *H. capillaricornis* ssp. *pisidicus* Korge est passé au rang d'espèce. Des Lectotypes sont désignés pour *Habrocerus capillaricornis* (Gravenhorst) et *H. schwarzi* Horn. *Nomimocerus tichomirovae* Filatova est transféré dans le genre *Habrocerus*. *H. magnus* Leconte d'Amérique du Nord est exclu du genre. 3 nouvelles espèces de *Nomimocerus* Coiffait & Saiz, dont on ne connaissait jusqu'à présent que l'espèce de type, *N. marginicollis* (Solier), sont décrites: *N. longispinosus* sp. n., *N. peckorum* sp. n., tous deux du Chili, et *N. parvispinosus* sp. n. d'Argentine et du Chili. La position systématique et les caractéristiques morphologiques, en particulier la structure de l'abdomen mâle, de *Habrocerus* et *Nomimocerus* sont présentées. Pour chaque espèce, des détails et des illustrations des caractères différentiels aussi bien que les dates de dispersion et, dans le cas où cela est possible, l'écologie sont présentés. Des clés permettent de déterminer les adultes d'*Habrocerus* et de *Nomimocerus*.

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A new earthworm (Ocnerodrilidae, Oligochaeta) from a Brazilian cave and considerations about *Belladrilus*.

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A new earthworm (Ocnerodrilidae, Oligochaeta) from a Brazilian cave and considerations about *Belladrilus*. - *Belladrilus* (*B.*) *otarion*, n.sp. is described from a cave in São Paulo State, Brazil. The excess of partner's spermatozoa is resorbed in the ental part of the spermathecal duct. The *Belladrilus* genus and its two subgenera (*Belladrilus* s.s. and *Santomesia*) are reevaluated. A key to *Belladrilus* species is presented.

Key-words: Oligochaeta - Ocnerodrilidae - *Belladrilus* - cave - Brazil.

INTRODUCTION

Interested in general cave fauna Dr. Eleonora Trajano (Depto. Zoology, University of São Paulo) collected some small earthworms in the Gruta dos Paiva (24°16' S-48°17' W), a cave in Iporanga Municipality, São Paulo State, Brazil, at February 2, 1989. The cave is located in a calcareous area, it is longer than its known 2,880 m and is composed of a main gallery throughout traversed by the Lageado River and an upper dry gallery with several outwards openings. The earthworms were found in the very damp calcareous silty-arenaceous sediments that form the river edges inside the cave. The associated fauna, mainly arthropods, is listed by TRAJANO & GNASPINI-NETTO (1991). I thank to Dr. Trajano for the opportunity to study the earthworms.

The earthworms were studied by dissections, pieces mounted on microscope slides with glycerin-water (1:1) and serial microscopical sections, 10 µm, stained by Mallory's triple method (PANTIN, 1964). The sketches were made with camera lucida. The material is deposited in the Department of Zoology, University of São Paulo (ZU) and in the Museum d'Histoire Naturelle, Genève (MHNG).

Belladrilus (B.) otarion n.sp.

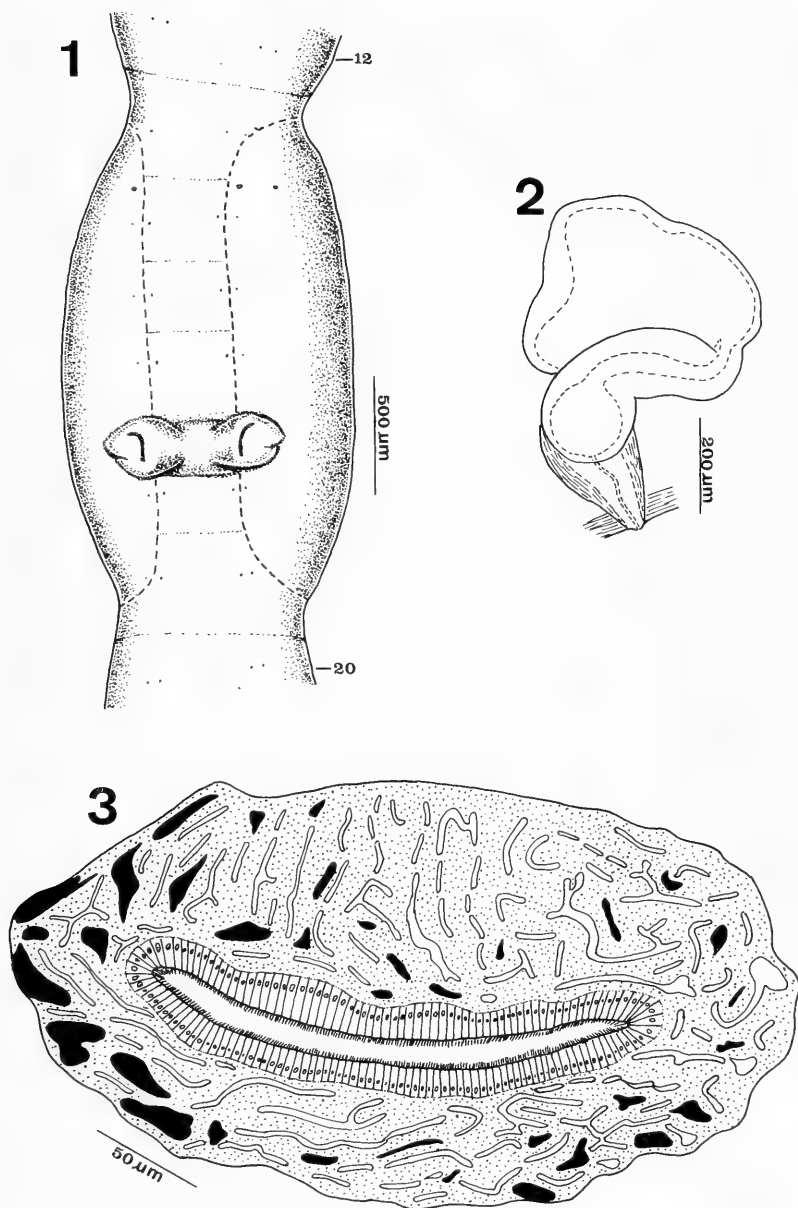
(Figs 1-3)

MATERIAL – Holotype: 1 clitellate specimen (ZU-1282A); paratypes: 2 clitellate specimens (MHNG-18880 INVE); 2 mature a clitellate and 2 young specimens (ZU-1282B).

DESCRIPTION – The length of the animals varies from 21-28 mm, the mid-body diameter from 0.9-1.0 mm and the number of segments from 65-72. They have not pigment. The prostomium is epilobous 1/3 of open tongue. There are not dorsal pores. There are 8 setae per segment beginning from II and disposed in 4 pairs of regular lengthwise series. The setal ratios in the middle body region (segments XXX-XL) are $aa : ab : bc : cd : dd = 5.7 : 1.0 : 5.7 : 1.0 : 19.0$ ($ab = 48 \mu\text{m}$). The mid-body setae are elongated sigmoid with distal nodule and unicuspidate apex of smooth surface without ornamentation. Their length varies from 112-128 μm ($M = 120 \mu\text{m}$), the longest ones are ventral. There are not differentiated genital setae; the mature animals have not the ventral setae of XVII. The clitellum extends on XIII-XIX (= 7 segments); it is saddle-shaped with the lower limit at ab . The tumid male genital field is ventral on 3/4 XVII-1/4 XVIII growing in angles at each side up to 1/3 bc . The male pores are in 17/18 on line b and the prostatic pores at 1/2 XVII a little lateral to b . The two pores of every side are connected by a seminal groove similar to an inverted L. The two areas of the male genital field containing the seminal grooves are prominent like two small ears with a lateral notch (Fig. 1). The female pores are anterior in XIV on line b . A pair of spermathecal pores is placed on small rounded papillae in 7/8, line b . Nephridiopores were not seen.

The septa 6/7-10/11 are thick and muscular, the septa 5/6 and 11/12 are a little less thick and the other septa are thin and fragile. Septal glands go up to VI. A rounded and strongly muscular gizzard lies in VII. There is a pair of thick tubular calciferous glands in IX; they originate from the lateral walls of the oesophagus close to septum 9/10 and go downwards and forwards to septum 8/9. Each gland has a large axial cavity and a thick wall (Fig. 3). The wall is composed by an intricate net of interconnected glandular canaliculi intermingled with blood spaces. The axial cavity is wide near to its opening into the oesophagus and becomes successively smaller towards the anterior end of the gland, where it receives the parietal glandular canaliculi. There is no other opening of the glandular canaliculi into the axial cavity. The wall of the axial cavity is formed by a high cylindrical ciliated epithelium without folds or trabeculae. The intestine begins in XII; caeca and typhlosolis are lacking. Two pairs of thick intestinal hearts are in X and XI. There is a pair of stomate avesculate nephridia per segment.

A pair of testes and iridescent male funnels lies in X, whose cavity is full of spermatozoa. There are two pairs of seminal vesicles in IX and XI; they have nodular surface and the first pair is somewhat smaller. The pair of male ducts proceed in a straight course laterally to the prostate duct to 17/18, where they pierce the body wall. The pair of prostate glands is in XVII; the glands are long and lie under the intestine being directed forwards to XII or backwards to XXVI. The duct of each gland is thin and muscular without ectal dilation and 2 1/2 segments long, it goes in a straight course forwards to XV or backwards to XIX. The transition from duct to glandular part is



FIGS 1-3

Belladrilus (B.) otarion: 1. Ventral view of the XII-XX segments. 2. Spermathecae (glycerin-water mounting). 3. Transverse section through the mid region of a calciferous gland.

sudden. The glandular part is tubular, 2-3 times wider than the corresponding duct, long and very sinuous. One pair of ovaries and female funnels are ventral in XIII; there are not ovisacs. One pair of spermathecae lies in VIII. They are S-bent formed by a long duct and a bulky pear-shaped ampulla. The duct is folded like an elbow with a dilation in the bend setting apart an ectal part from an ental one. The ectal part of the duct is almost half as long; its wall is thickly muscular and its thin lumen lacks spermatozoa. The dilation is simple, without seminal chambers and it may or may not have some spermatozoa. The ental part of the duct has a wide lumen filled with spermatozoa. Its wall is made up of large club-shaped cells of basal nucleus and homogeneously pale blue stained plasma with pieces of bright red stained spermatozoa in reabsorption. The ampulla, full of spermatozoa, has glandular walls.

DISCUSSION – *B. (B.) otarion* shares with *B. (B.) arua* the morphology of the seminal grooves and a similar morphology of spermathecae, with well differentiated duct and ampulla. The two species are distinguished by the following characteristics: *B. (B.) otarion*: male pores in 17/18 (*B. (B.) arua*: male pores in 1/2 XVIII); spermathecal pores in 7/8 (in 8/9); two pairs of seminal vesicles in IX and XI (one pair in XI).

ETYMOLOGY – The name of the new species refers to the shape of the male porophores in the plural genitive of the classical Greek word $\tau\omicron\ \omega\tau\alpha\rho\iota\omicron\nu$ = small ear.

CONSIDERATIONS ABOUT THE GENUS *Belladrilus*

The genus *Belladrilus* Righi includes originally two subgenera: *Belladrilus* s.s. and *Santomesia* Righi (1984a). Due to the discovery of *B. (B.) otarion*, with male pores in 17/18 and one pair of spermathecae in 7/8, the distinction between the two subgenera becomes restricted to the structure of the calciferous glands as emphasized in the key below.

KEY TO *Belladrilus* SPECIES (DISTRIBUTIONAL DATA AFTER RIGHI 1984A, B AND MISCHIS 1991)

1. Cavity of the calciferous glands with longitudinal trabeculae not coalescing in the gland axis or cavity simple, without trabecula. *Belladrilus* s.s. . 2
- Cavity of the calciferous glands divided by lengthwise trabeculae coalescing in the gland axis. (Prostate pores in 1/2 XVII and male pores in 17/18; spermathecal pores in 8/9, line *b*. Argentina: Santa Fe and Cor-doba prov.). *Belladrilus (Santomesia) emiliani* Righi, 1984a
2. Prostate pores in 1/2 XVII and male pores in 1/2 XVIII; spermathecal pores in 8/9. 3
- Prostate pores in 1/2 XVII and male pores in 17/18; spermathecal pores in 7/8, line *b*. (Brazil: São Paulo State). *B. (B.) otarion*, n.sp.
3. Spermathecal pores in line *b* (Brazil: Mato Grosso State).
. *B. (B.) pocaju* Righi, 1984a

- Spermathecal pores in line c. 4
- 4. Seminal grooves straight. Sac-like spermathecae without distinction between duct and ampulla (Argentina: Corrientes and Cordoba prov.). *B. (B.) jimi* Righi, 1984a
- Seminal grooves like an inverted L. Spermathecae with long duct folded in elbow and well separated egg-like ampulla (Brazil: Mato Grosso State). *B. (B.) arua* Righi, 1984b

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On the genus *Eurostoptinus* Pic, 1895 (Coleoptera, Ptinidae)

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On the genus *Eurostoptinus* Pic, 1895 (Coleoptera, Ptinidae) – The genus *Eurostoptinus*, and its constituent species, *E. algericus* (Pic) and *E. mazuri* sp. n., are redescribed or, respectively, described. In general appearance these species resemble members of the genus *Pseudeurostus* Heyden (= *Eurostus* Muls. & Rey), particularly *P. submetallicus* (Fairmaire). The new species may be distinguished by the pronotal microsculpture.

Key-words: Coleoptera - Ptinidae - *Eurostoptinus* - Algeria.

INTRODUCTION

PIC (1895) based a new subgenus of *Eurostus* Muls. & Rey, *Eurostoptinus*, on a new species from Algeria, *E. algericus*. Later, *Eurostoptinus* was treated as a genus (Pic, 1907; 1912). It appears related to *Pseudeurostus* Heyden (= *Eurostus* Muls. & Rey) but may be readily distinguished by the pronotal shape, pubescence and microsculpture, and by the elytral shape. In a collection made recently in Algeria, a second member of *Eurostoptinus* was present. This species is new and described below. The range of the genus, including two apterous species, is possibly restricted to Algeria.

The type and other examined material are deposited in the Muséum d'histoire naturelle, Geneva.

Eurostoptinus Pic, 1895

Eurostus Muls. & Rey sg. *Eurostoptinus*; type species: *Eurostus algericus* Pic, 1895, by monotypy.

Length 2-3.2 mm. Body black or dark brown. Abdomen redish-brown. Dorsal and ventral surface covered by yellow pubescence. Labrum, legs and abdomen brown or reddish, with pubescence thicker than that on most of the body surface. Antennal

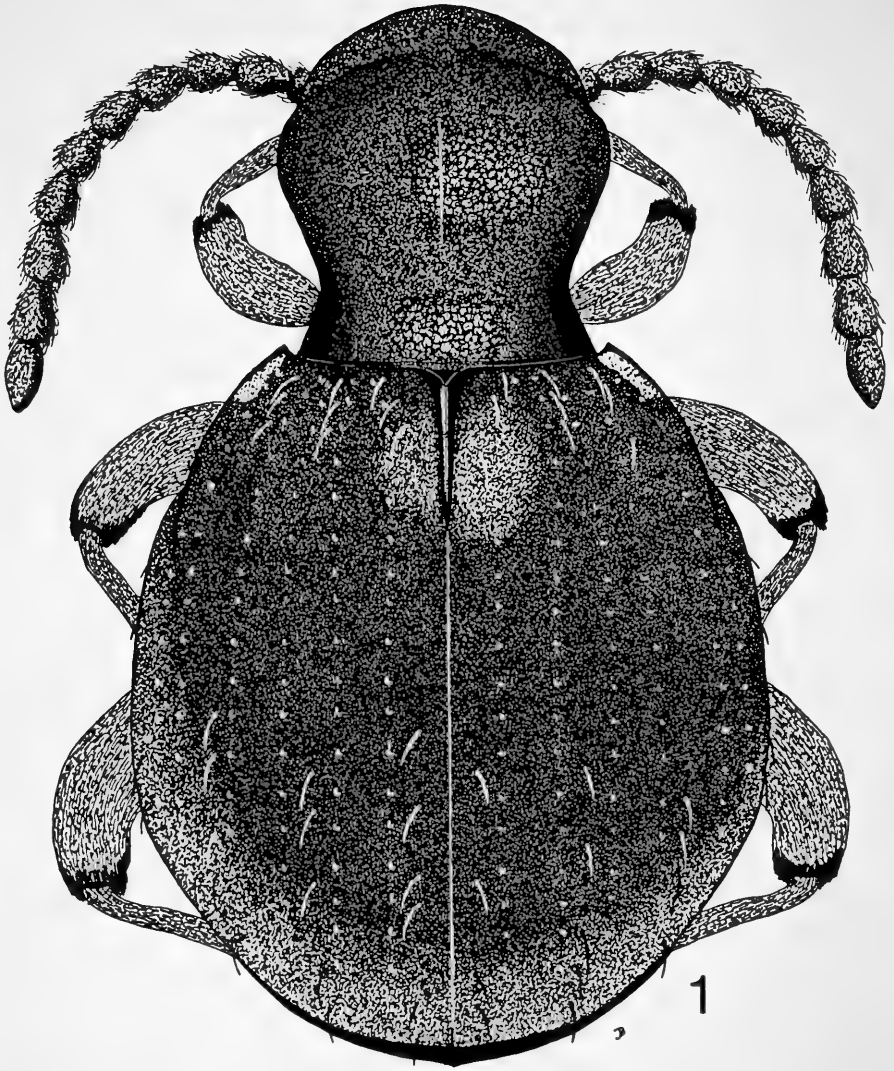


FIG. 1

Eurostoptinus mazuri n. sp.: dorsal view.

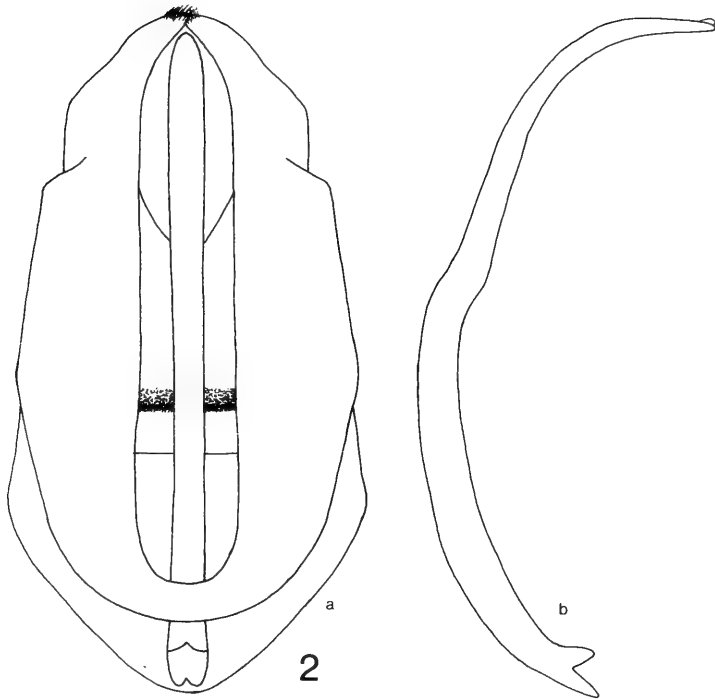


FIG. 2

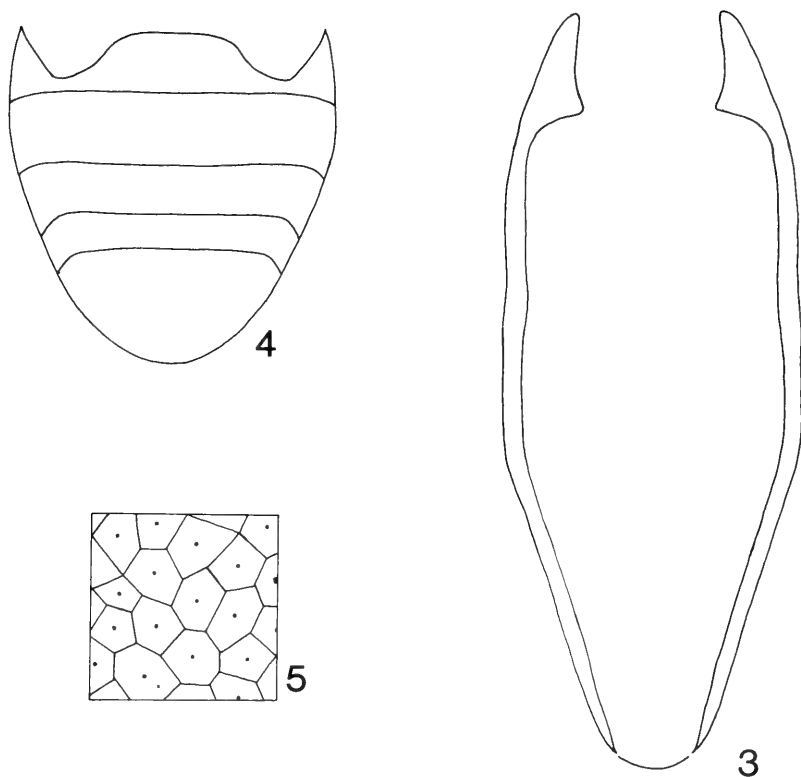
Eurostoptinus mazuri n. sp.: aedeagus (a), median lobe (b).

segments short, with pubescence thickest near base, becoming gradually shorter toward apex. Head elongate, with sparse pubescence. Antennal fossae deep, with sharp upper edge and sharpened asides. Eyes small. Pronotum with two blunt lateral callosities; pubescence absent or sparse on anterior side; pronotal microsculpture polygonal or consisting of flat verucae. Scutellum small, triangular. Elytra convex, shiny, narrowed toward apex; anterior angles strongly extended forward, humeral callosity distinct, elytral pubescence irregular, thicker on base and apex, present only on even intervals; discal striae faintly marked, sutural margin raised anteriorly. Metathoracic wings absent.

***Eurostoptinus algericus* (Pic, 1895)**

(Figs 6 to 9)

DESCRIPTION: Length 2-2.5 mm. Body dorsally black, shiny, with sparse pubescence. Head brown, antennae and legs reddish. Ventral side of body entirely pubescent, dark brown, apical abdominal segment reddish. Pronotum with rounded lateral callosities.



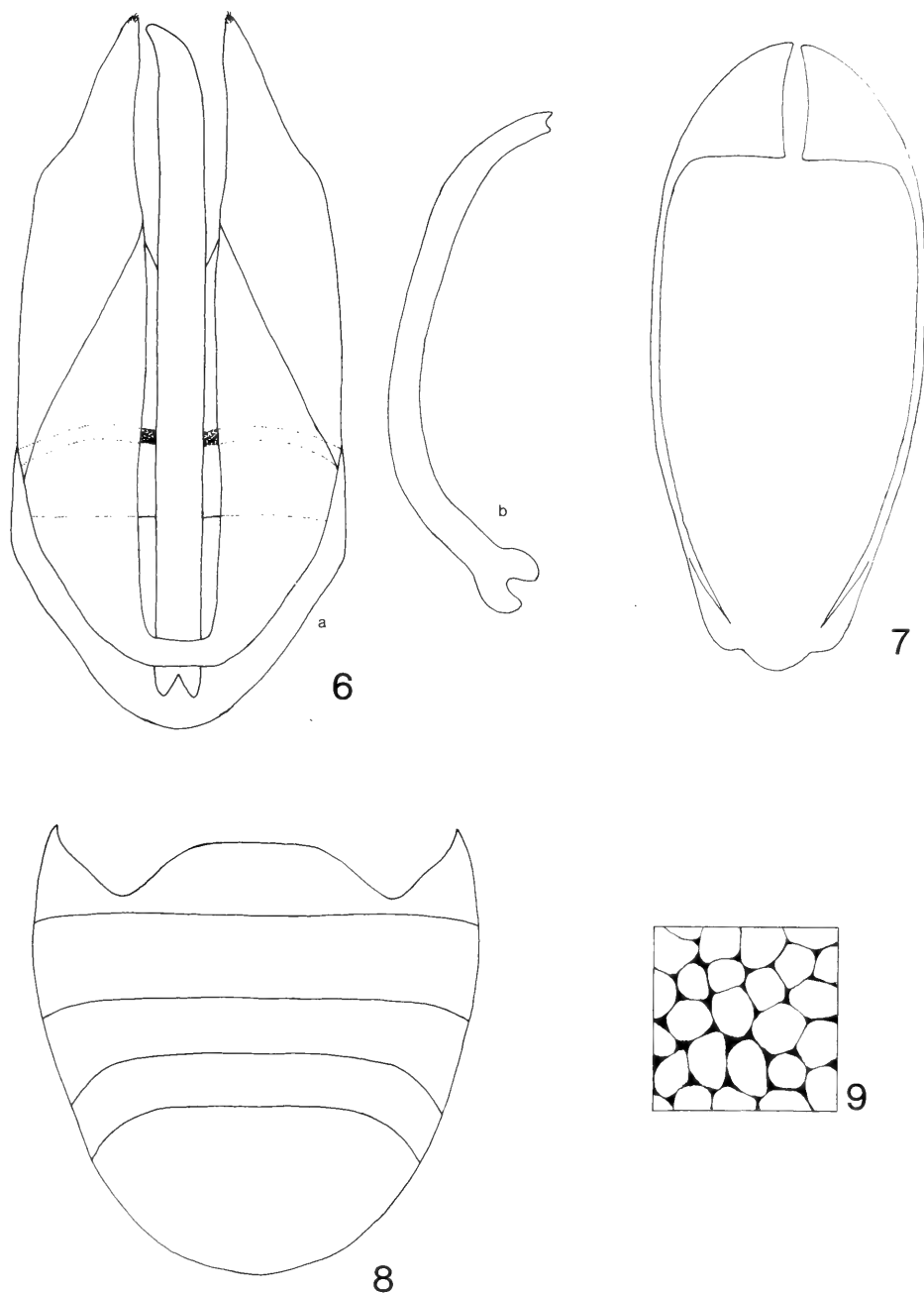
FIGS 3-5

Eurostoptinus mazuri n. sp.: male genital segment (3), visible abdominal sternites (4), sculpture surface of pronotum (5).

Pronotal microsculpture consisting of flattened verrucae (Fig. 9); discal pubescence absent, pubescence on anterior surface sparse. Scutellum hardly visible. Elytra short, shiny, with hardly visible rows of punctures, latter shallow, fairly distant from each other. Free abdominal ventrites 3 and 4 of same length (Fig. 8). Male genital segment as Fig. 7. Aedeagus with symmetrical parameres (Fig. 6).

DISTRIBUTION: Algeria (recorded by Pic, 1907 from: Collo, Tigzirt, Yakouren, Azazga, Djurdjura, Djebel, Babor, Cap Aokas).

MATERIAL EXAMINED: Algeria, Yakouren, 730 m, 12.V.1988, leg. Burckhardt, Löbl, Besuchet, 1 specimen; Forêt d'Akfadou, 13 km from Yakouren, 1050 m, 16.V.1988, leg. Burckhardt, Löbl, Besuchet, 1 specimen.



FIGS 6-9

Eurostoptinus algericus (Pic): aedeagus (6a), median lobe (6b), male genital segment (7), visible abdominal sternites (8), sculpture surface of pronotum (9).

Eurostoptinus mazuri sp. n.

(Figs 1 to 5)

DESCRIPTION: Length 3.2 mm. Body black, ventrally blackish-brown; shiny, covered by sparse pubescence. Head somewhat narrower than pronotum, with short pubescence. Eyes small, hardly prominent. Pronotum with two large lateral callosities, hardly convex in middle, median groove narrow. Anterior side of pronotum with few hairs. Pronotal microsculpture distinct, polygonal, with fine points in centers (Fig. 5). Scutellum small. Elytra convex, narrowed apically, with marked humeral ridge. Elytral pubescence very fine, mostly present on anterior and posterior surface; yellowish hairs present on lateroposterior edge. Free abdominal ventrite 3 distinctly longer than 4 (Fig. 4). Male genital segment as Fig. 3. Aedeagus symmetrical, as Fig. 2.

HOLOTYPE, male: Algeria, Djurjura, Tikjda, 1430 m, 6.V.1988, leg. Burckhardt, Löbl, Besuchet.

PARATYPE, female: Algeria, Djurjura, Tala Guilef, 1300 m, 11.V.1988, leg. Burckhardt, Löbl, Besuchet.

REMARKS: The new species may be distinguished from *E. algericus* by the large size of the body, the microsculpture of the pronotum and the shape of the aedeagus. Both, *E. mazuri* and *E. algericus* inhabit oak forests of Grand Kabilia. Specimens collected by the Geneva entomologist's are from sifted moist forest litter.

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PIC, M., 1912. Ptinidae. *Coleopterorum Catalogus*. 41. W. Junk, Berlin, 46 pp.

**Two new cave Prosobranch snails from Papua New Guinea:
Selmistomia beroni n.gen. n.sp. (Caenogastropoda: Hydrobiidae) and
Georissa papuana n.sp. (Archaeogastropoda: Hydrocenidae).
(Zoological results of the British Speleological Expedition to Papua
New Guinea 1975.)**

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Two new cave Prosobranch snails from Papua New Guinea: *Selmistomia beroni* n.gen. n.sp. (Caenogastropoda: Hydrobiidae) and *Georissa papuana* n.sp. (Archaeogastropoda: Hydrocenidae). - (Zoological results of the British Speleological Expedition to Papua New Guinea 1975.) Conchyliological and anatomical data of two new snails found in caves of Western province of Papua New Guinea are given. *Selmistomia beroni* n.gen.n.sp. is described from Selminum Tem cave, *Georissa papuana* n.sp. is described from Big Cave.

Key-words: Hydrobiidae - Hydrocenidae - Papua New Guinea - New taxa.

INTRODUCTION

A British speleological expedition spent 5 months in 1975 exploring an area of 25'000 sq.km. of limestone terrain of Finim Tel Plateau in the Central Highlands, Papua New Guinea, and culminated in the discovery and exploration of the 20 km long Selminum Tem cave. The cave fauna collected by P. Beron and P. Chapman included a number of troglomorphic and endemic new species (CHAPMAN 1985) which have been described between 1977 and 1992. The Molluscs collected in two caves and entrusted to me in August 1993 by P. Beron are listed in this paper and two new taxa are described.

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SPECIES ACCOUNT

Selminum Tem Cave, Western Province PNG.

- Prosobranchia Hydrobiidae Tateinae : *Selmistomia beroni* n.gen. n.sp.
Approx. 40 specimens of a new species living in water. See description below.
- Pulmonata Planorbidae : *Segmentina* sp.
One non adult specimen; indetermined.

Big Cave, Western Province PNG.

- Prosobranchia Hydrocenidae: *Georissa papuana* n.sp.
Approx. 40 specimens of a new species living on wet rock. See description below.
- Prosobranchia Hydrobiidae Tateinae : *Fluviopupa* sp. or *Selmistomia* sp.
Two specimens, only empty shells; not determinable.

DESCRIPTIONS

***Selmistomia* n.gen.**

DIAGNOSIS: Member of the subfamily Tateinae; *Hemistomia* - like pupoid - ovate shell. Operculum with a non - calcareous , non - digitate peg, the peg is bent over about 90° toward the external edge of the operculum; the peg is concentrically striated. Penis bearing in the middle part a crest - like lobe. Radula central teeth with 2 pairs of basal cusps.

TYPE SPECIES: *Selmistomia beroni* n.sp.

Derivatio nominis: Selminum Tem Cave, Western Province PNG.

Selmistomia is closely related to *Hemistomia* Crosse 1872, *Fluviopupa* Pilsbry 1911 and *Fluvidona* Iredale 1937 (= *Hemistomia* sensu PONDER 1982).

For discussion on systematics: See PONDER & WAREN 1988, and KABAT & HERSHLER 1993.

DIFFERENTIAL DIAGNOSIS:

Other similar genera of the "*Hemistomia* radiation" sensu PONDER 1991 differ from *Selmistomia* as follows:

(a) genera with 1-2 pairs of basal cusps on the central teeth of the radula (no difference with *Selmistomia*):

- *Hemistomia* Crosse 1872: possesses an orange operculum with a 2-4 digitate straight peg and white smear, without concentric striae (FRANC 1956, SOLEM 1961); the soft part anatomy is astonishingly not yet known; possibly a monotypic endemic New Caledonian genus (PONDER 1991, PONDER 1992).

- *Jardinella* Iredale & Whitley 1938: possesses an operculum with or without a white smear, no peg; an elongated osphradium; a simple penis with or without swollen areas; a pallial vas deferens with loops or coils. (PONDER & CLARK 1990).
- *Fonscochlea* Ponder, Hershler & Jenkins 1989: possesses an operculum with small white smear; and /or with a 2-5 digitate peg; a simple, evenly tapering penis, without lobe or bulb; a renal oviduct with two equal - sized sperm sacs. (PONDER et al. 1989).

(b) genera with 3-5 pairs of basal cusps on the central teeth of the radula:

- *Fluvidona* Iredale 1937 (= *Hemistomia* sensu PONDER 1982): possesses an operculum with a white smear and a mostly 2-5 digitate, straight peg; a simple, evenly tapering penis, without lobe or bulb (PONDER 1982).
- *Fluviopupa* Pilsbry 1911: possesses a thin horny paucispiral operculum with white smear, but no pegs; a distally lobed penis, some species with a median bulb; a straight intestine on pallial roof (PONDER 1982, STARMÜHLNER 1970, SOLEM 1959, HUBENDICK 1952, ANCEY 1905).
- *Potamopyrgus* Stimpson 1865: possesses an operculum with or without white smear, no peg; a simple, tapering penis, without lobe; the females are sometimes ovoviviparous; sometimes parthenogenic reproduction (PONDER 1982, PONDER & CLARK 1990).
- *Tatea* Tenison-Woods 1879 possesses an operculum with a 2-10 digitate peg; a simple penis without lobe; in the females a genital opening located beneath the middle of the capsule gland; a partially spirally sculptured shell with two protoconchs (PONDER et al. 1991).

Selmistomia beroni n.sp.

MATERIAL:

Holotype: Museum of Natural History of Geneva, Switzerland, N° MHNG 994.104

L = 2.92 mm; Dmax. 1.69 mm; Ratio L/Dmax = 1.73; 4 1/2 whorls, Aperture 0.94 x 0.81 mm.

Paratypes: Museum of Natural History of Geneva, Switzerland N° MHNG 994.105 (7); National Museum of Natural History, Sofia, Bulgaria (7); my collection.

Type locality: freshwater stream in the cave Selminum Tem, Finim Tel Plateau, near Telefomin, Central Highlands, Hindenburg Range, Western Province, Papua New Guinea. Selminum Tem cave system develops 20,5 km of passages at an altitude of 2400 m a.s.l. Air temperature in the cave was 13°C; Aug. 1975, P. Beron and P. Chapman

SHELL (fig.1): the shell is minute pupoid - ovate, with 4 to 4,5 rounded whorls, both protoconch and teloconch are smooth. Without columellar fold, without umbilicus. Aperture ovate separated from parietal wall by a narrow groove, peristome continuous and little thickened.

Dimensions of the type series (holotype + 26 paratypes ; n=27):

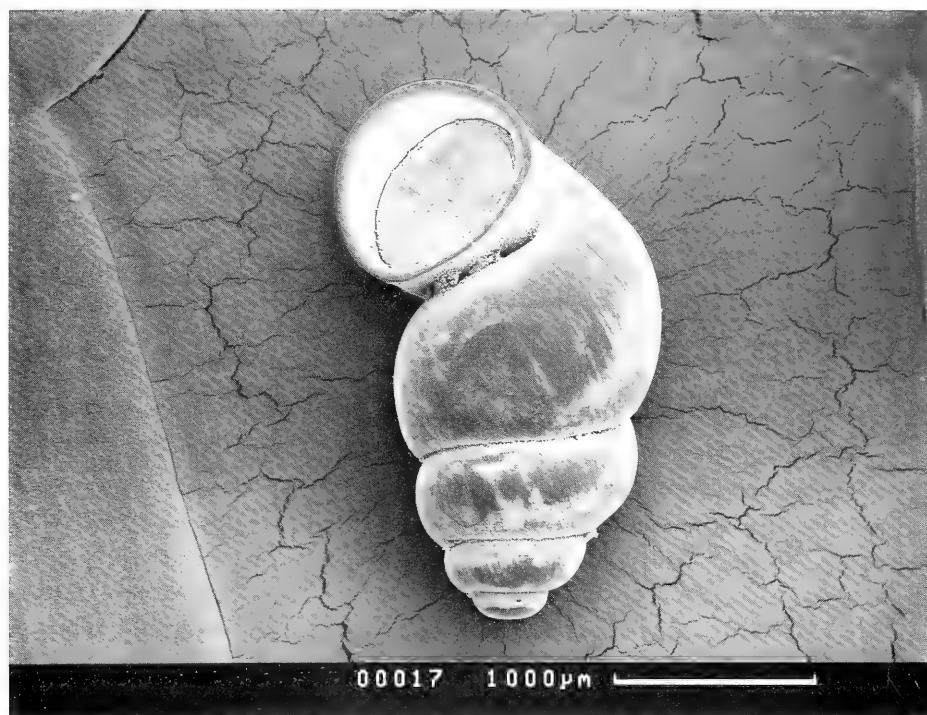


FIG. 1

Selmistomia beroni: shell.

length L: 2.47 mm ; standard deviation SD 0.23 mm

min. 2.08 mm ; max. 2.92 mm

diameter max. (shell width) Dmax.: 1.44 mm ; SD 0.13 mm;

min: 1.23 mm; max. 1.72 mm

diameter of last whorl D1: 1.21 mm ; SD 0.10 mm

min. 1.01 mm; max. 1.46 mm

Ratio L/Dmax.: 1.72 ; SD 0.08

min. 1.55 ; max. 1.90

Ratio L/D1.: 2.04 ; SD 0.13

min. 1.74 ; max. 2.28

HEAD-FOOT: Without pigment. Cephalic tentacles with eye spots at their basis. Operculum (fig.2): subovate (770 - 815 x 540 - 520 μ m) with a peg (140 -200 μ m in height), its edge is sinuous but not subdivided in fingers, the peg is bent over about 90° toward the external edge of the operculum. No white smear.

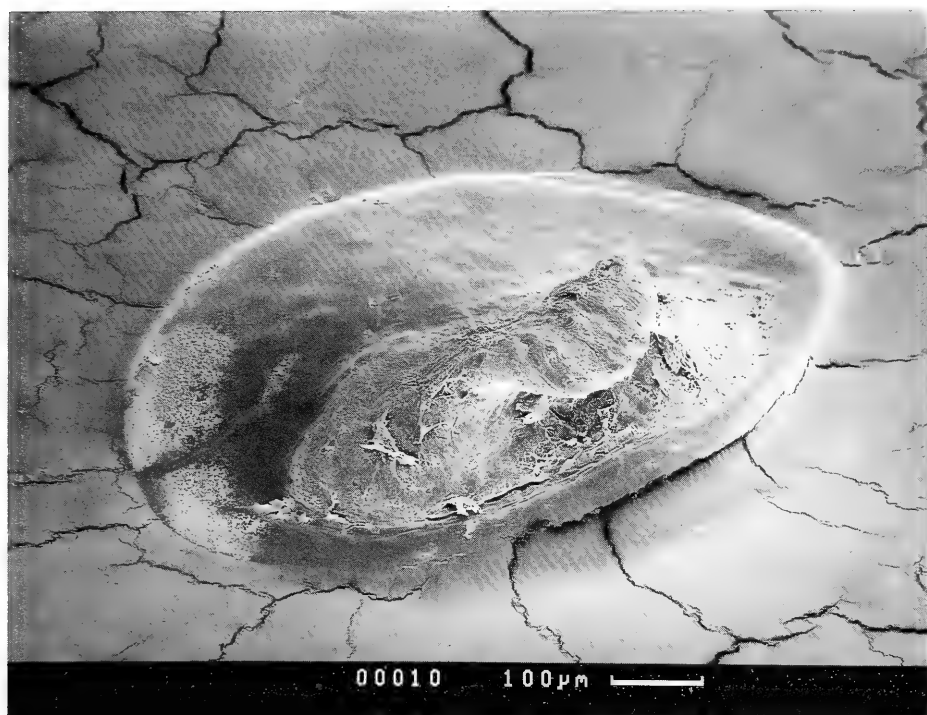


FIG. 2

Selmistomia beroni: operculum.

Radula (fig. 3): taenioglossate typically amnicolid with the formula $5+1+5/2+2$; $4+1+5$; 24; 22. The marginal and lateral teeth are about $45\text{ }\mu\text{m}$ long, the central tooth is trapezoidal $20\text{ }\mu\text{m}$ large. The radula size is about $500 \times 60\text{ }\mu\text{m}$.

MANTLE CAVITY (fig. 4): mantle edge without papilla. Ctenidium with 7-10 gills. Osphradium short, oval ($200 \times 90\text{ }\mu\text{m}$).

DIGESTIVE SYSTEM: Stomach with style sac; no coecal appendage. Intestine makes a pallial S-shaped double loop on pallial roof, and contains ovate faecal pellets.

FEMALE REPRODUCTIVE SYSTEM (fig.4): Capsule gland composed of two parts. Renal oviduct thickens and makes a double loop, insert one small Seminal Receptacle ($100 \times 105\text{ }\mu\text{m}$) and enters the ventral channel. An elongate Bursa copulatrix ($520 \times 250\text{ }\mu\text{m}$) is connected with a short duct with central insertion to the ventral channel at the inferior end of albumen gland. Ducts of Bursa copulatrix and Seminal Receptacle became distended before their insertion to the ventral channel. The ventral channel opens at the end of capsule gland. No gonopericardial duct detected.

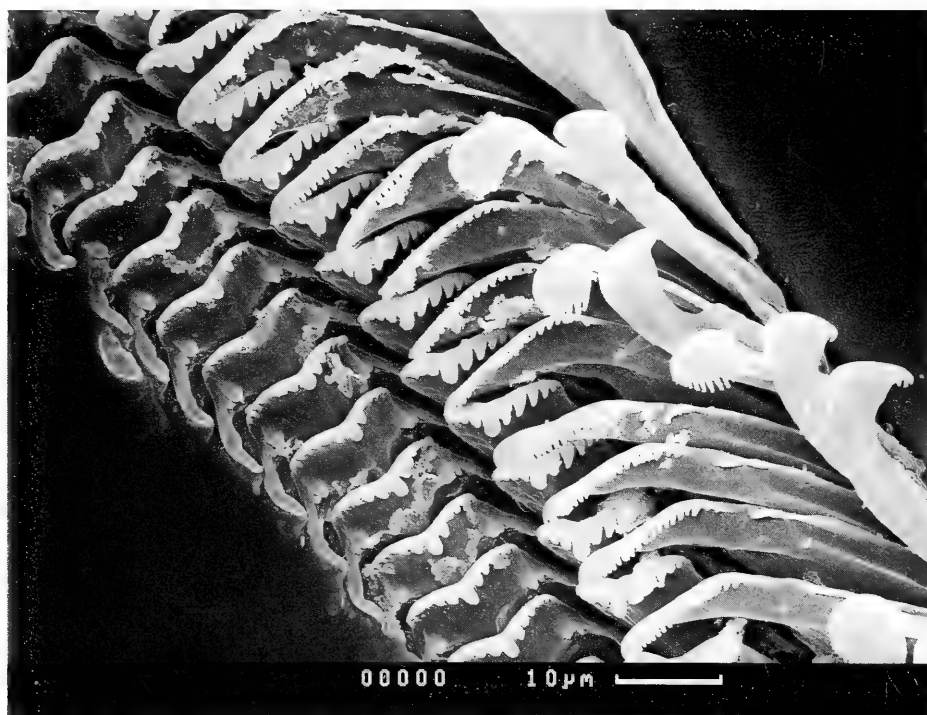


FIG. 3

Selmistomia beroni: radula.

MALE REPRODUCTIVE SYSTEM (fig.4): Penis conical about 1000 μm long, expanded base, tapering to slender distal end; a crest - like lobe (90 x 55 μm) at its middle part. Prostate bean-shaped (700 x 270 μm). Pallial vas deferens straight or undulating, no loops.

ETHYMOLOGY: named after Dr. Petar Beron, director of the National Museum of Natural History, Sofia, who entrusted the specimens to me.

From Papua New Guinea only few taxa of possible Hydrobiidae were known previously:

"*Hemistomia*" *pygmaea* Van Benthem Jutting 1963, known only by the shell; the 2.5 mm long shell has a thick calcareous rib along the exterior margin of the peristome.

"*Tatea*" *pyramidata* Van Benthem Jutting 1963, known only by the shell; after PONDER et al. 1991 this species being probably a member of Pomatiopsidae.

"*Fluviopupa*" *novoguineensis* Van Benthem Jutting 1963, was described from West Irian (PNG) only on shell characters; after PONDER 1982 this species is not a *Fluviopupa* but is identical with "*Tatea*" *pyramidata*.

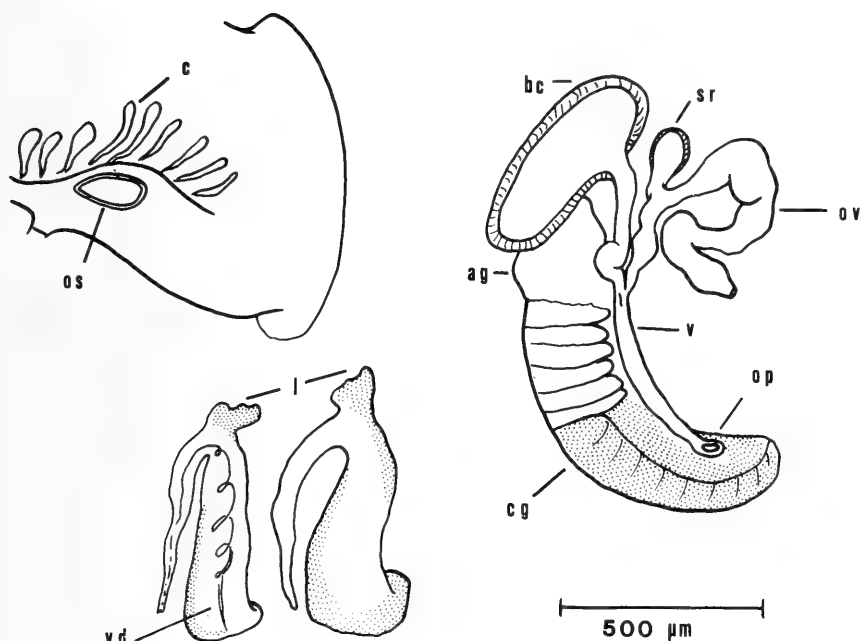


FIG. 4

Selmistomia beroni: mantle cavity: c - ctenidial filaments; os - osphradium; male reproductive system (penis): l - penial lobe; vd - vas deferens; female reproductive system (oviduct complex): ag - albumen gland; bc - bursa copulatrix; cg - capsule gland; ov - oviduct; op - oviduct opening; sr - seminal receptacle; v - ventral channel.

Two specimens of *Fluviopupa* - like hydrobiids from the Sepik River are known from empty shell only (PONDER 1982).

Previous works (RIECH 1937) on molluscs of Papuaia and Melanesia do not mention any representative of Hydrobiidae.

None of the above cited genera or species can be identified with the specimens from Selminum Tem Cave.

Selmistomia beroni is therefore the first unequivocal representative of Hydrobiidae known on the island of New Guinea.

***Georissa papuana* n.sp.**

MATERIAL:

Holotype: Museum of Natural History of Geneva, Switzerland, N° MHNG 994.102.

L= 1.73 mm; Dmax. 1.52 mm; Ratio L/Dmax = 1.14; 3 1/4 whorls, Aperture 0.75 x 0.75 mm.

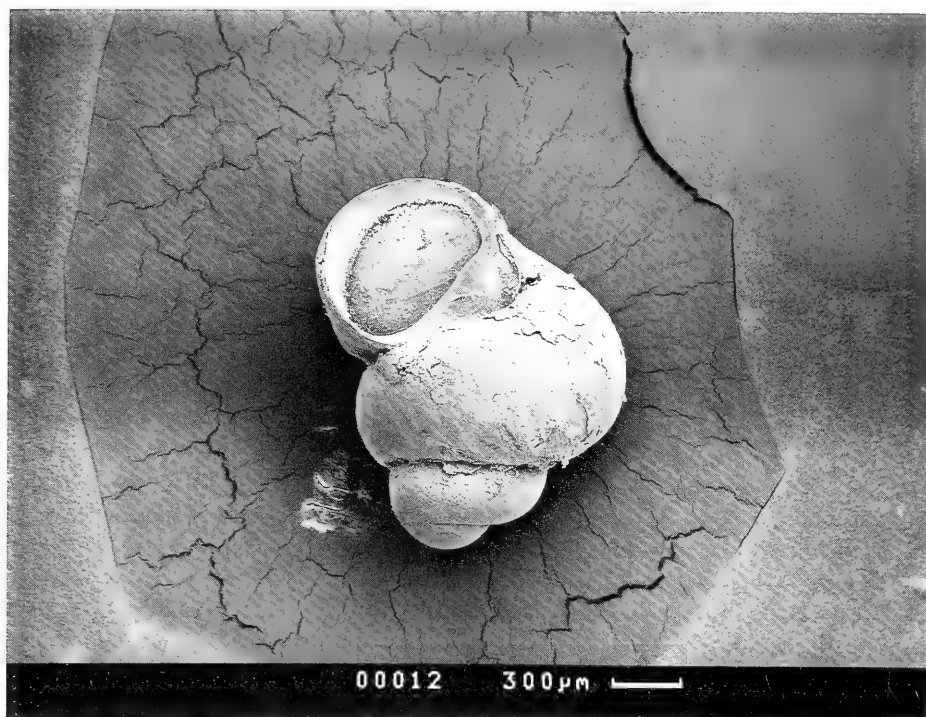


FIG. 5

Georissa papuana: shell.

Paratypes: Museum of Natural History of Geneva, Switzerland (N° MHNG 994.103) (6); National Museum of Natural History, Sofia, Bulgaria (6); my collection.

Type locality: Big Cave, Mount Fugilil, Finim Tel Plateau, Central highlands, Western Province, Papua New Guinea. Big Cave opens at an altitude of 3100 m a.s.l. Air temperature in the cave was 9°C; Aug. 1975, P. Beron and P. Chapman, .

SHELL (fig.5): Shell minute broadly conical, with 3.5 to 4 rounded whorls. Apex rounded with a large cap - shaped spherical smooth protoconch. Teloconch smooth, in juvenile and transparent specimens there are weakly developed longitudinal brown ribs between growth striations crossing hardly detectable, very weak spiral threads. Without umbilicus, umbilical area closed with a wide shield (or callus). Columellar callus wide and rounded. Aperture subovate, peristome thin.

Dimensions of the type series (holotype + 24 paratypes; n=25) :

length L: 1.69 mm ; standard deviation SD 0.08 mm

min. 1.56 mm ; max. 1.85 mm

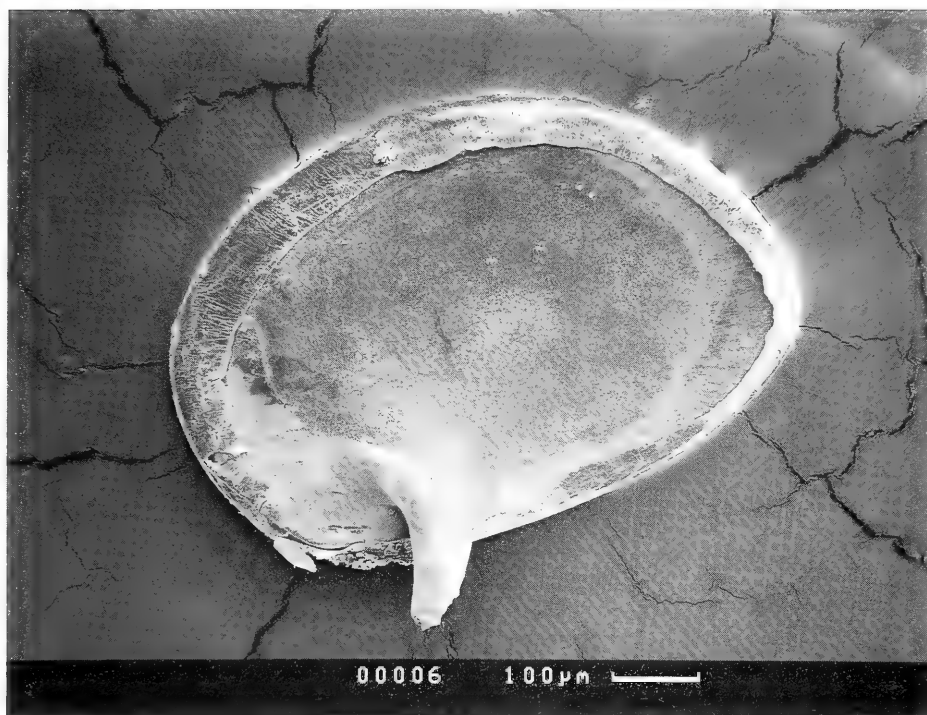


FIG. 6

Georissa papuana: operculum.

diameter max. (shell width) Dmax.: 1.40mm ; SD 0.05 mm;

min: 1.30 mm; max. 1.46 mm

diameter of last whorl D1: 1.21 mm ; SD 0.06 mm

min. 1.10 mm; max. 1.33 mm

Ratio L/Dmax.: 1.21 ; SD 0.04

min. 1.09 ; max. 1.27

Ratio L/D1.: 1.40 ; SD 0.07

min. 1.32 ; max. 1.54

HEAD-FOOT: Snout short and broad, almost unpigmented. No cephalic tentacles; the large eyes are sessile at the basis of short cephalic lobes.

Operculum (fig.6): subovate (approx. 700 x 480 μm) formed by an outer horny plate with concentric striations and an inner calcareous plate, smooth, bearing an acentric stocky peg (apophysis) (approx. 240 μm in height) close to the columellar edge of the operculum; the peg is slightly bent and projects outwards, its dorsal side has a longitudinal groove. The inside edge of the operculum bears a narrow circular callus.

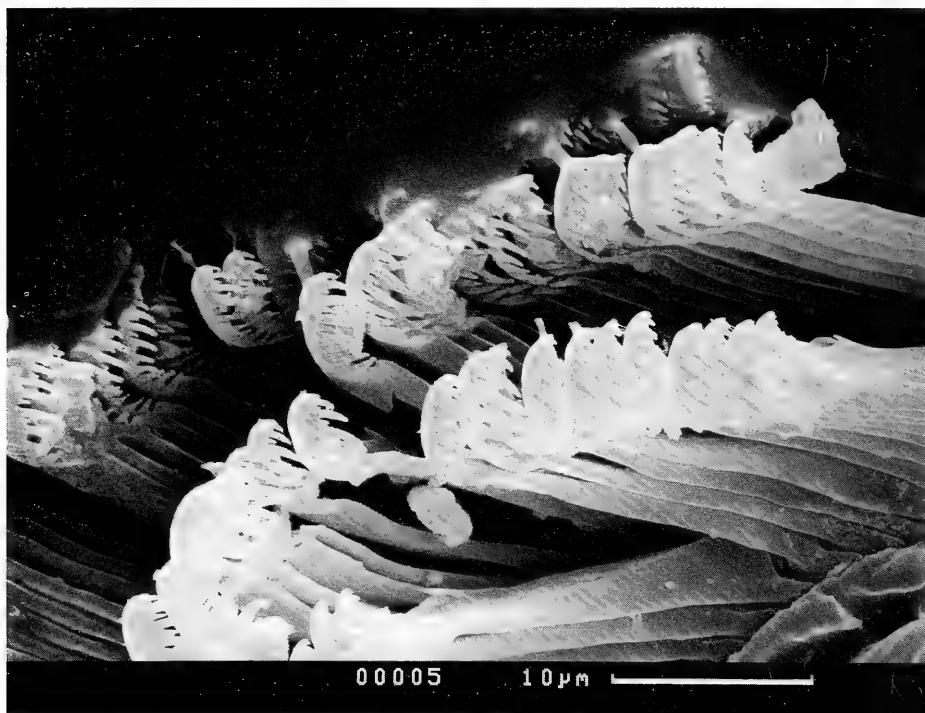


FIG. 7

Georissa papuana: radula.

The operculum is retractable within the mouth of the shell, its upper edge retracts within the shell for about a quarter whorl.

Radula (fig.7): rhipidoglossate. Very long radular sac ($1100 \times 60 \mu\text{m}$ to $2200 \mu\text{m} \times 100 \mu\text{m}$); the about 1000 mm long radula consists of approx. 14 cords of very numerous marginal teeth approx. $27 \mu\text{m}$ long; the edge of these marginal teeth bears about 10 long cusps alternating with about 8 short cusps. Central and lateral teeth missing.

MANTLE CAVITY: mantle edge without papilla. No gills; no osphradium. Mantle wall vascularized.

DIGESTIVE SYSTEM (fig.8): No jaw. Oesophagus (diameter approx. $50 \mu\text{m}$) from radular sac to stomach. Stomach (approx. $425 \times 275 \mu\text{m}$) with style sac (approx. $345 \times 205 \mu\text{m}$); no coecal appendage. Intestine (diameter $95 \mu\text{m}$) makes a double loop around the style sac, and moves straight to its opening in the pallial cavity (pallial rectum); the intestine contains a few ovate faecal pellets in the vicinity of the stomach and a pulpy brown faecal mass in the pallial rectum. Subsequently to the stomach a large sized, brown orange coloured digestive gland.

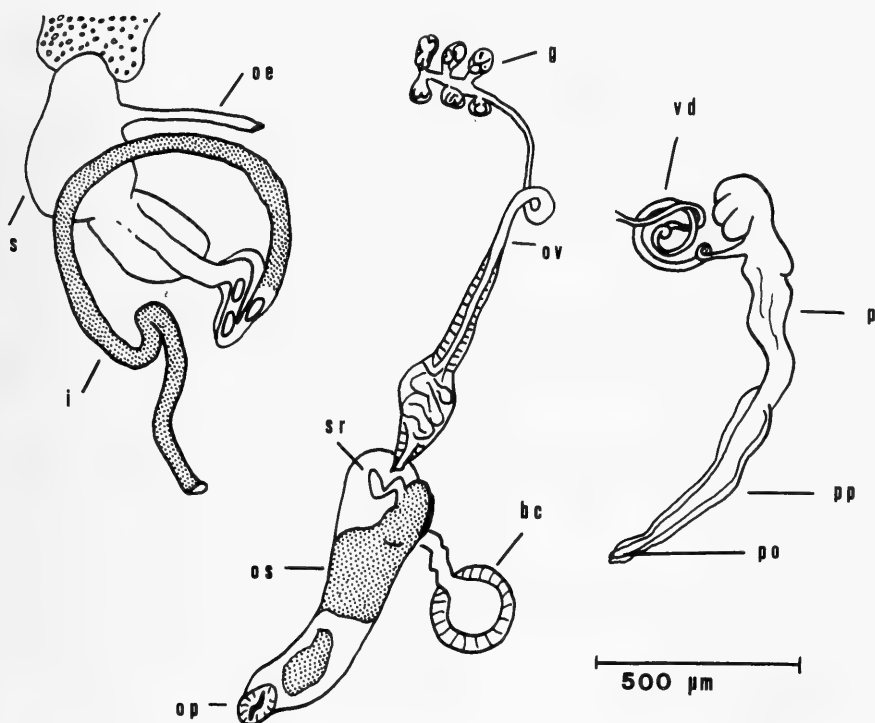


FIG. 8

Georissa papuana: digestive system: i - intestine; oe - oesophagus; s - stomach; female reproductive system (oviduct complex): bc - bursa copulatrix; g - gonad; os - oviduct sac; op - oviduct opening; ov - oviduct; sr - seminal receptacle (?); male reproductive system (prostate complex): p - prostate I; pp - prostate II; po - prostate opening; vd - vas deferens.

FEMALE REPRODUCTIVE SYSTEM (fig.8): a pallial oviduct sac (approx. $700 \times 200 \mu\text{m}$) (uterus ?, nidamental gland ?) opens near the opening of the intestine. The renal oviduct becomes a glandular wall and thickens before its opening into the upper section of the uterus. A spherical Bursa copulatrix (approx. $200 \times 170 \mu\text{m}$) inserts through a bursal duct in the upper part of the uterus. On the opposite side a little tubular lobe (approx. $120 \times 35 \mu\text{m}$) (seminal receptacle ?) enters also the uterus. The upper part of the uterus wall is thickened and glandular; the lumens occupy a little more than $3/5$ of the upper, posterior part and $1/5$ of the lower, anterior part.

MALE REPRODUCTIVE SYSTEM (fig.8): No copulatory organ. The very elongated prostate (approx. $1000 \mu\text{m}$ long) lies along the pallial intestine portion (pallial rectum), it opens near the opening of the intestine; the prostate is formed by a long glandular section (approx. $900 \times 100 \mu\text{m}$) (spermatophore organ ? prostate II ? anterior prostate ?) and a short glandular section (approx. $380 \times 170 \mu\text{m}$) around the opening of the vas deferens (cytaphore organ ? prostate I ? prostate I ? posterior prostate ?). The vas deferens makes a lot of coils before the testes.

ETHYMOLOGY: named after Papua country.

DIFFERENTIAL DIAGNOSIS:

Georissa papuana differs from other similar Hydrocenid species as follows:

- from all *Georissa* species described from the Pacific and Asiatic areas having sculptured conch (spiral threads, spiral nodes); for instance *G. sarrita* Benson (BLANFORD 1869); *G. javana* Moellendorf 1897 (VAN BENTHEM JUTTING 1948); *G. zea* (THOMPSON & ILIFFE 1987); *G. (=Omphalorissa* Iredale 1933) *multilirata* Brazier 1875, *G. minuta* Odhner 1917, *G. postulata* Iredale 1937, *G. laseroni* Iredale 1937 and *G. obesa* (SOLEM 1988); *G. williamsi*, *G. hosei*, both Dowin-Auten 1889; *G. similis*, *G. gomantonensis*, both Smith 1893; *G. borneensis*, *G. everetti*, both Smith 1895; *G. kobelti* Gredler 1902; *G. hadra*, *G. pyrrhoderma*, *G. xesta* (THOMPSON & DANCE 1984).

Other species described as *Hydrocena* are indeed sculptured *Georissa*, e.g. *H. reticulata* (VAN BENTHEM JUTTING 1957); *H. quadricarinata* (VAN BENTHEM JUTTING 1963); *H. scalinella* and *H. saulae* (VAN BENTHEM JUTTING 1966).

- only few *Georissa* species with obliterated sculpture have been described: *Realia* (= *Georissa*) *isseliana* (Tapparone-Canefri 1883) (SOLEM 1988); *G. laeviuscula* Moellendorf 1897 and *G. obsoleta* (THOMPSON & HUCK 1985]. *G. isseliana* from Aru Island, Papua New Guinea, differs from *G. beroni* in having a subacute apex and a conical shell (operculum unknown); *G. laeviuscula* from Java lacks an umbilical shield; *G. obsoleta* from the New Hebrides possesses a more conical shell and weak denticles above shoulder along the second and third whorls.
- *Lapidaria chinensis* (Kang 1986) from China differs in radula, intestine and shell characters.
- *Georissops* Pilsbry & Hirase 1908 from China differs by a non-retractable operculum within the mouth of the shell.
- *Chondrella* Pease 1871 from Society Island differs by a heavy callused ridge around the inside margin of the operculum.
- *Hydrocena* L.Pfeiffer 1847 from Europe differs by a conical smooth shell, by the operculum apophysis and some anatomical characters (BLANFORD 1869) (THIELE 1910).

From Papua New Guinea only one species, *Georissa isseliana* (Tapparone-Canefri 1883), was known till now; and from West New Guinea only two species: *Hydrocena reticulata* Van Benthem Jutting 1958 and *H. quadricarinata* Van Benthem Jutting 1963.

None of the above cited taxa can be identified with the specimens from Big Cave.

The finding of a *Georissa* in a cave is not inhabitual, as the species of this genus live on limestone or in association with calcareous terrain (THOMPSON & DANCE 1984), often on the soil of damp forest (VAN BENTHEM JUTTING 1948) or in caves (SAUL 1966).

Three species were described from caves in Borneo: *Hydrocena scalinella* and *H. saulae* in Sabah province, *Georissa pyrrhoderma* in Sarawak province.

No less inhabitual is the finding of *Georissa* species at high altitudes: *Hydrocena javana* and *H. laeviuscula* were found at Mt. Gedeh, Java, at 3000 m.a.s.l. (VAN BENTHEM JUTTING 1948).

Astonishingly all the recent Hydrocenid species were described only on shell characteristics; no soft part anatomy has been described, except those for *Georissa sarrita* Benson by BLANFORD 1869 and for *Hydrocena cattaroensis* Pfeiffer 1841 by THIELE 1910.

An anatomical comparison with other Hydrocenid genera of which no anatomical data are known is not possible. Therefore the Hydrocenid of Big Cave is tentatively assigned to the genus *Georissa*, accordingly SOLEM 1988 stating that "the name *Georissa* is used for all Pacific taxa".

In a recent revision of proserpinoid snails, THOMPSON 1980 suggested for the Hydrocenidae the new superfamily Hydrocenacea TROSCHEL 1856 within the Neritimorpha.

ACKNOWLEDGEMENTS

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Terrestrial isopod crustaceans (Oniscidea) from Paraguay with definition of a new family

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Terrestrial isopod crustaceans (Oniscidea) from Paraguay with definition of a new family. – The Oniscidea from Paraguay are reviewed. New taxa are *Paraguascia pigmentata* n. gen. n. sp., *Alboscia elongata* n. gen. n. sp., *Novamundoniscus* n. gen. (for *Phalloniscus vandeli* Lemos de Castro). Dubioniscidae n. fam. (proposed for *Calycuoniscus*, *Dubioniscus* and *Novamundoniscus* n. gen.). Characters of examined previously described taxa are discussed, detailed redescrptions are given for *Dubioniscus delamarei* and *Trichorhina brasiliensis*. *Circoniscus* is briefly reviewed along with a record of *C. bezzii* from Paraguay. *Venezillo bolivianus* is briefly redescrbed. Fifteen species of terrestrial Oniscidea are recorded from Paraguay, four of which are cosmopolitan. *Trichorhina heterophthalma* is recorded for the first time from Paraguay.

Key-words: Oniscidea - Dubioniscidae n. fam. - *Phalloniscus* - Paraguay.

INTRODUCTION

Terrestrial isopods were first recorded from Paraguay by DOLLFUS (1894) who discussed five species including two new ones. Subsequently he gave (1897) additional information on Paraguayan and some other species from Argentina and Bolivia. As the Chaco region was in dispute between Paraguay and Bolivia at this time, some of Dollfus's records might be from present day Bolivia. VAN NAME (1936) described *Philoscia paraguayana* from Paraguay and gave short notes on species described by Dollfus. ANDERSSON (1960) added a further oniscidean species to the fauna of Paraguay and discussed a few others. VANDEL (1963) transferred *P. paraguayana* to *Balloniscus* because all five pairs of exopods of the pleopods contain pseudotrachea. In the absence of new material of *Balloniscus paraguayanus*, *B. sellowi* and of *Benthana picta*, the discussion below are based only on facts from the literature.

Dubioniscus delamarei, described by VANDEL (1963) from Argentina, was collected in Paraguay. It is made the basis of a new family. *Phalloniscus vandeli* Lemos de Castro from Brazil was reencountered and redescrbed. The species is represent here at most of the stations sampled and by most of the specimens. It and

other members of *Phallonicus* from the New World are placed in a new genus here. *Phallonicus*, *Calycuoniscus* and *Dubioniscus* have been variously placed in Bathytropidae, Oniscidae or Platyarthridae, but here *Dubioniscus*, *Calycuoniscus* and the new genus defined here are placed in a new family based on *Dubioniscus*. The anophthalmic, now known to be common, species of *Trichorhina brasiliensis*, is redescribed. A recent summary of the species in *Circoniscus* briefly is reviewed and *C. bezzii* is recorded at one station in Paraguay. Three species of Armadillidae, including the common *Cubaris murina* and two, one new, species of *Venezillo* are discussed.

Three tiny specimens of Trichoniscidae (Buddelundiellinae, perhaps in *Buchnerillo*) were collected 80 km S Bella Vista (Amambay prov. sifting of forest litter. 1.XI.1979), but they were too small (almost 1 mm long, one damaged) to be identified further or discussed here. Four species of common oniscideans which are cosmopolitan in distribution were collected in Paraguay, their ranges now formally include Paraguay: *Cubaris murina*, *Porcellionides pruinosus*, *Porcellio laevis* and *Trichorhina heterophthalma*. It is of interest to note that *Cubaris murina* and *Trichorhina heterophthalma* generally are recorded to be widespread in subtropical and tropical habitats, whereas *Porcellio laevis* is more abundant in temperate habitats. *Porcellionides pruinosus* has been recorded in tropical, subtropical and temperate habitats, and perhaps is the most widely distributed oniscidean in the world. All 15 named Oniscidea from Paraguay are recorded in their respective family in Table 1.

Two of the four expansive and/or cosmopolitan species recorded are discussed briefly below in their respective family. The two other species belonging to Porcellionidae are in *Porcellio laevis* recorded by DOLLFUS (1894) from Tresistencia, Chaco, and Asuncion, and *Porcellionides pruinosus* recorded as a *Metoponorthus* by DOLLFUS (loc. cit.) from Buenos Aires, Argentina, and Villarrica and Asuncion, Paraguay. They were cited by ANDERSSON (1960) and VANDEL (1962a).

MATERIAL

All oniscideans described and discussed here were collected during the Zoological Expeditions to Paraguay carried out by the staff of the Muséum d'histoire naturelle in 1979 and 1982. The type specimens of the new species and other specimens described or redescribed here are deposited in the museum (MHNG). Example specimens of several species (see individual accounts) have been donated to the National Museum of Natural History (Smithsonian Institution) (USNM), and the Natural History Museum London (BMNH). Lemos de Castro deposited his specimens in the Museo Nacional, Rio de Janeiro (MNRJ).

PHILOSCIIDAE

In his comprehensive work on the Oniscidea of France, VANDEL (1962a:503) defined Philosciinae which he included as a subfamily in Oniscidae. Philosciinae later was raised to family, but Vandel's definition still is the best of the taxon to date.

TABLE 1

All 15 Named Oniscidea Recorded from Paraguay
(with family placement)

Cosmopolitan Species

- Cubaris murina* (Brandt, 1833) (Armadillidae) (not collected)
Porcellio laevis Latreille, 1804 (Porcellionidae) (not collected)
Porcellionides pruinosus (Brandt, 1833) (Porcellionidae) (not collected)
Trichorhina heterophthalma Lemos de Castro, 1964 (Platyarthridae)

Endemic Species

- Alboscia elongata* n. gen. n. sp. (Philosciidae)
Balloniscus paraguayanus (Van Name, 1936) (Balloniscidae) (not collected)
Balloniscus sellowii (Brandt, 1833) (Balloniscidae) (not collected)
Benthana picta (Brandt, 1833) (Philosciidae) (not collected)
Dubioniscus delamarei Vandel, 1963 (Dubioniscidae n. fam.)
Circoniscus bezzii Arcangeli, 1931 (Scleropactidae)
Novamundoniscus n. gen. *vandeli* (Lemos de Castro, 1959) (Dubioniscidae n. fam.)
Paraguascia pigmentata n. gen. n. sp. (Philosciidae)
Trichorhina brasiliensis Andreasson, 1960 (Platyarthridae)
Venezillo bellavistanus n. sp. (Armadillidae)
Venezillo bolivianus (Dollfus, 1897) (Armadillidae)

(Three tiny, damaged specimens of Trichoniscidae, perhaps *Buchnerillo* of Buddelundiellinae, were collected but not described.)

Benthana picta, redescribed by GRUNER (1955), was recorded from Villarrica, Paraguay, by ANDERSSON (1960:559). The two new species of Philosciidae collected in Paraguay differ morphologically. One has large eyes and a shiny, darkly pigmented dorsum; the other has small eyes and a shiny, pigmentless dorsum. All definitions of genera and unresolved, poor descriptions of philosciids from the New World were examined and comparisons were made with the specimens described here. No species or genus of Philosciidae recorded from the New World conforms in character presence or absence to the two new species so each was placed in a separate genus. Since many species of Philosciidae from the New World have been so poorly described any many are to be described in the future, some important characters to be used for describing species and defining genera of philosciids are as follows:

Absence or presence and number of ocelli

Size of anterolateral lobes on cephalon

Absence or presence and type of frontal and supra-antennal lines

Dorsum with or without small scales

Absence, presence or degree of body pigment

Pattern and number of aesthetascs on antenna 1

Absence or presence and pattern of lateral nodes and glands on pereons

Mandibular type and setation, especially type of setation on molar (single, few, compounds), number in setal row and on lacinia mobilis

Type and number of teeth on exopod of maxilla 1
Absence or presence of penicillate setae on blade of maxilliped
Type of grooming organ on pereopod I (and II) of male and female
Width of pleon compared to width of pereon
Type and length of neopleurons on pleonal segments
Absence or presence and type and number of pseudotracheae on exopods of pleopods
Shape of uropods including whether rami come off at same or different level
Shape, especially posterior margin, of pleotelson.

Paraguascia n. gen.

DIAGNOSIS. Eyed. Supra-antennal line well developed. Pigmented dorsum smooth. Lateral nodes present. Molar of mandible compound. No penicillate setae on blade of maxilliped. Pereopods I of male and female with conspicuous grooming organs. Two spots on outer surface of basis of pereopods collectively appear as two darkened lines in ventral view of specimen. Pleon abruptly narrower than pereon; neopleurons of segments 4 to 5 closely appressed laterally. Pseudotracheae absent. Rami of uropods arise at same level.

TYPE SPECIES. *Paraguascia pigmentata* n. sp. Type by original designation. Gender. Feminine.

TAXONOMIC REMARKS. The new genus is near to *Prosekia* Vandel (1968), but that genus is composed of a diverse set of eight species (see LEMOS DE CASTRO & SOUZA, 1989). The new genus differs from the type of *Prosekia*, *P. galapagensis*, in that it has few aesthetascs on antenna 1, a compound molar on the mandible, no penicillate seta on the maxilliped and the rami of the uropods arise at the same level. The general shape of the palp of the maxilliped (two bundles of setae on article 2 arise directly from the edge; they are not mounted on extensions of the edge) is different when compared to the shape of the palp recorded for other species of *Prosekia*. According to the criteria listed above for Philosciidae, when the species of *Prosekia* are reexamined representative of several genera will be revealed.

Paraguascia pigmentata n. sp.

Figs 1A-L and 2A-S

DESCRIPTION. About 12 ocelli. Body about twice as long as broad. Dorsum smooth, shiny and variegated dark brown. Lateral nodes each with long seta visible on edges of pereons I to III and V to VII (Fig. 1A). Glands on pereons not apparent. Cephalon set in front of pereon I; anterolateral lobes small; distinct frontal and supra-antennal lines. Antenna 1 with four long aesthetascs two in first tier and two apically placed. Antenna 2 extending back about to posterior edge of pereon III; flagellum longer than

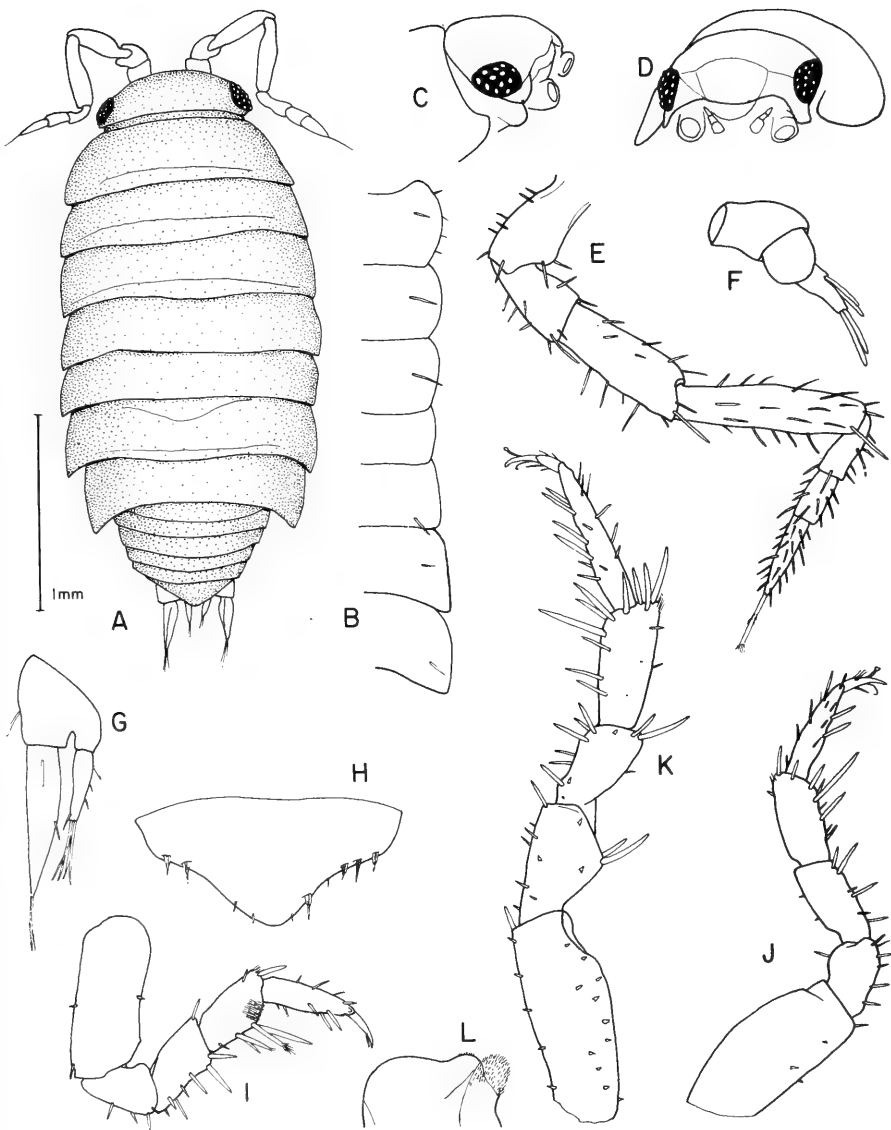


FIG. 1

Paraguascia pigmentata n. gen. n. sp.: A) dorsal view; B) detail, edges of pereopods; C) cephalon, lateral view; D) cephalon, frontal oblique view; E) antenna 2; F) antenna 1; G) uropod; H) pleotelson; I) male pereopod I; J) male pereopod II; K) male pereopod VI; L) tip maxilla 2.

peduncle segment 5, three articles subequal in length, apical article tipped with long seta.

Labrum rounded. Left and right mandibles with compound molar, one seta in setal row and one seta on lacinia mobilis. Exopod of maxilla 1 with four simple large outer teeth and four smaller inner bifurcate teeth; endopod with apex round and two subapically placed penicillate setae. Maxilla 2 with narrow, rounded sensory lobe projecting medially from square apex. Maxilliped with few setae on outer surface; blade lacks penicillate seta; basal segment of palp with large seta on inner margin and smaller seta laterally; inner margin of edge of second segment with two bunches of setae and apical segment with tuft of setae. Epipod about 2/3 length of maxilliped proper, apex rounded.

Pereon with convex lateral margins. All pereopods with long dactylar organ with knob on end. Grooming organ formed as propodus with two large setae distally on inner surface and very long setae on inner surface of carpus. Female pereopod I with few setae on inner surface of propodus; dactylus with grooming organ and with many elongate setae on inner surface; long distally placed setae on outer surface of dactylus and merus.

Pleon narrower than pereon; segment 1 with edges suppressed by pereon VII; segments 2 to 5 with neopleurons laterally appressed to pleon. Genital apophysis simple. Male pleopod 1 with exopod with medial edge only slightly produced, apex rounded; no marginal setae; endopod simple, produced and apex folded laterally. Male pleopod 2 with exopod moderately elongate, two marginal setae; endopod elongate, thin and pointed. Female pleopod with exopod tiny, medially produced, no marginal setae. Male pleopods 3 to 5 and female pleopods 2 to 5 simple with many marginal setae. Pleotelson with posterolateral margins excuvate, posterior margin rounded. Long rami of uropod exiting at same level, basis deeply notched between exit sites of rami; endopod about half as long as exopod; each tipped with few long setae.

Measurements. To about 4 mm long.

TYPE LOCALITY. Misiones prov. 30 km San Juan Bautista (road to San Ignacio) near Ao. Aguaray, sifting forest litter, 14.X.1982: 1 male (holotype).

DISTRIBUTION. Caaguazu prov., 20 km N Colonel Oviedo, sifting bamboo leaves, 7.X.1979, 2 paratypes females (females lost) during.

The sympatric *Novamundoniscus vandeli* can be distinguished by the presence of two lines of pigment on the basis of the pereopods.

Deposition of type and other specimens: MHNG.

Alboscia n. gen.

DIAGNOSIS. Eyed. Frontal line absent. Supra-antennal line present. Pigmentless, shiny body markedly narrower than long. Conspicuous lateral nodes present. Pleon slightly narrower than pereon. Pleonal segment 1 and part of segment 2 enclosed within broadly curved posterior margin of pereon VII; neopleurons of 2 to 5 closely appressed to pleon. Molar of mandibles compound. No penicillate setae on blade of

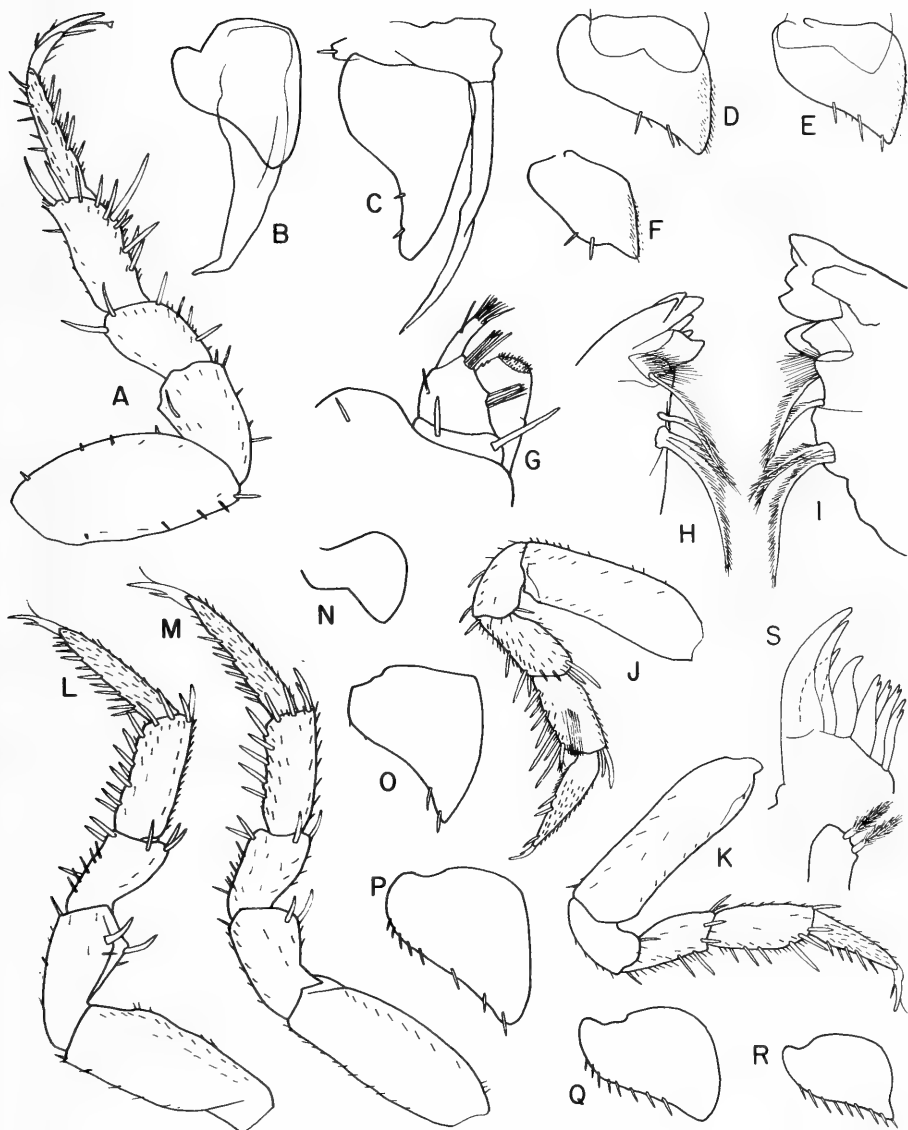


FIG. 2

Paraguascia pigmentata n. gen. n. sp.: A) male pereopod VII; B) male pleopod 1; C) male pleopod 2; D) male pleopod 3; E) male pleopod 4; F) male pleopod 5; G) detail maxilliped; H) left mandible; I) right mandible; J) female pereopod I; K) female pereopod II; L) female pereopod VI; M) female pereopod VII; N) female pleopod 1; O) female pleopod 2; P) female pleopod 3; Q) female pleopod 4; R) female pleopod 5; S) maxilla 1.

appressed to pleon. Molar of mandibles compound. No penicillate setae on blade of maxilliped.

TYPE SPECIES. *Alboscia elongata* n. sp. Type by original designation.
Gender. Feminine.

TAXONOMIC REMARKS. Species of several genera of Philosciidae from caves lack ocelli and all body pigment. Other philosciids, mainly from dense leaf litter or loose soil, have a reduced number of ocelli and little or no body pigment. The combed teeth on the exopod of maxilla 1 suggest that the new genus is related to *Benthana*. However, in addition to the combed teeth, all species of *Benthana* have many ocelli and are well pigmented, among other differences (see GRUNER, 1955).

***Alboscia elongata* n. sp.**

Figs 3A-J and 4A-T

DESCRIPTION. One ocellus (lens) apparent, but pigment pattern looks like three merged ocelli. Body about 3.25 times as long as broad. Cephalon set in front of pereon I. Dorsum smooth, shiny, without body pigment, but with some marginal setae on posterior borders of pleonal segments. Frontal margin of cephalon (dorsal view) slightly produced, anterolateral lobes moderately large, directed ventrally. Frontal line absent. Supra-antennal line well defined. Antenna 1 with apical article ending in large scale-like point with at least five aesthetascs in lower tier and two apically placed. Antenna 2 long and thin, if extended posteriorwardly it reaches about to posterior edge of pereon V. Flagellum of three articles about length of peduncular segment 5; middle article about half as long as articles 1 and 3. Article 3 tipped with long seta.

Labrum rounded. Left mandible with compound molar, one seta in setal row and many setae on molar. Right mandible with compound molar, one seta in setal row and no molar setae. Maxilla 1 with exopod with five outer plain teeth; four inner teeth combed; endopod apically rounded with two subapical penicillate setae. Maxilla 2 with inner sensory lobe about half width of rounded apex. Maxilliped with few scaled setae on outer surface; blade with one seta on outer margin and two triangulate scales on curved margin. Palp of maxilliped with two long setae on basal segment; segment 2 with two large setae close together on upper part of rounded inner margin; apical segment narrow, conical and about as long as both long setae on segment 2, apex tipped with several long setae. Epipod of maxilliped about 2/3 length of maxilliped proper, apically rounded.

Pereon with shiny surface, lateral margins more or less parallel. Pereon VII with posterolateral angles greatly produced with sinuate posterior margin. Lateral nodes with long seta visible (dorsal view - Fig. 3A) except on III; glands not apparent. All pereopods with simple dactylar organ. All pereopods of male and female similar.

Pleon slightly narrower than pereon. Edges of segment 1 enclosed within sinuate posterior margin of pereon VII; edges of segments 2 to 5 closely appressed to pleon. Genital apophysis simple. Male pleopod 1 with exopod broadly oval with to

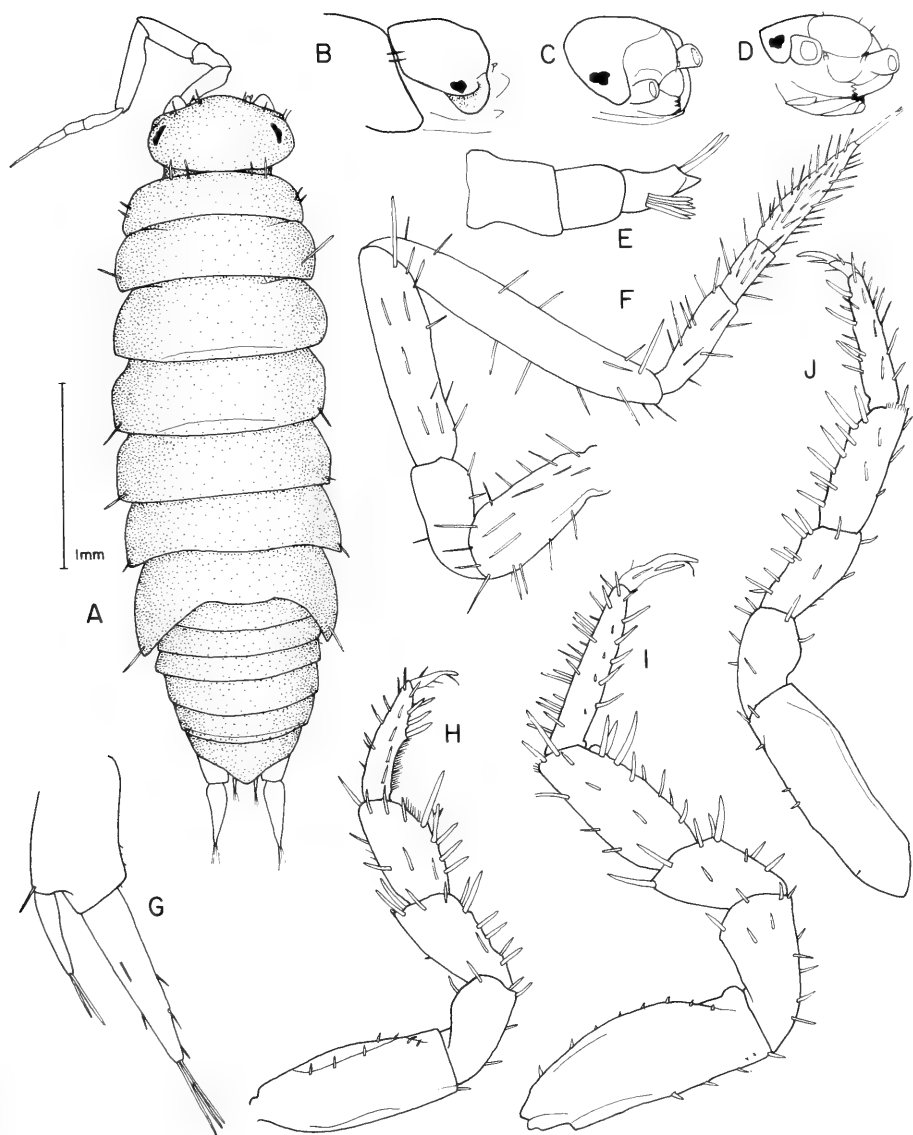


FIG. 3

Alboscia elongata n. gen. n. sp.: A) dorsal view; B) cephalon, lateral view; C) cephalon, oblique view; D) cephalon, ventral oblique view; E) antenna 1; F) antenna 2; G) uropod; H) male pereopod I; I) male pereopod II; J) male pereopod VI.

marginal setae; endopod elongate, moderately curved apically. Male pleopod 2 with exopod about half length of elongate, thin, pointed endopod; exopod with three setae on posterolateral margin. Male pleopods 3 to 5 and female pleopods 2 to 5 with one or few marginal setae. Pleotelson plain, posterolateral margins slightly concave; posterior margin obtusely pointed. Uropod with basis only partially projecting from under pleotelson; endopod about half length of exopod and set on basis well ahead of exopod. Both rami tipped with few long setae.

Measurements. Male to 3.6 mm long.

TYPE LOCALITY. Concepcion prov. between Est. Estrellas and Est. Primavera, sifting forest litter, 16.X.1979: 2 males; 1 female (holotype male and paratypes).

DISTRIBUTION. Known only from the type locality.

Deposition of type and other specimens: MHNG.

REMARKS. The integument of *A. elongata* is thin so it must live in moist habitats. The species superficially resembles *Colombophiloscia alticola* from the Galapagos Islands as described by VANDEL (1968:98). That small, pigmentless species with few ocelli has a simple molar on the mandible, four plain and four bifurcate teeth on the tip of the endopod of maxilla 1 and a rounded posterior margin on the pleotelson. PAULIAN DE FELICE (1944) described *Philoscia gracilior* from French Guiana. It is proportionately longer than the species described here and its antennae 2 and uropods are especially elongate. It has large eyes, but the number of ocelli is unknown. Also the mouth parts, pereopods or pleopods were not described. The species probably is in a new genus, but its inclusion in Philosciidae has not been confirmed.

BALLONISCIDAE

Balloniscidae which had no representatives in the collection was separated from Philosciidae by VANDEL (1963:83) because of the presence of five pairs of pseudotracheae. *Plataoniscus*, based on *Alloniscus borellii* Dollfus (1897) from Argentina and Bolivia, the second genus in the family, was defined by Vandel on specimens which also had five pairs of flattened pseudotracheae similar to those in species of *Balloniscus*. VANDEL (1963:86) also placed *Alloniscus griseus* Dollfus (1897) and *Porcellio argentinus* Giambiagi de Calabrese (1939) all from Argentina in *Plataoniscus*. Members of *Plataoniscus* have a vertex dividing the frontal line and an indistinct supra-antennal line according to Vandel. *Balloniscus paraguayanus* was redescribed by Lemos de Castro (1958). LEMOS DE CASTRO (1976) reviewed much information on species of *Balloniscus* and he removed *Plataoniscus argentinus* from the genus and placed it in synonymy with *Balloniscus sellowii* which he then illustrated.

The two species of *Balloniscus* from Paraguay are:

Balloniscus Budde-Lund, 1908

Balloniscus paraguayanus (Van Name, 1936)

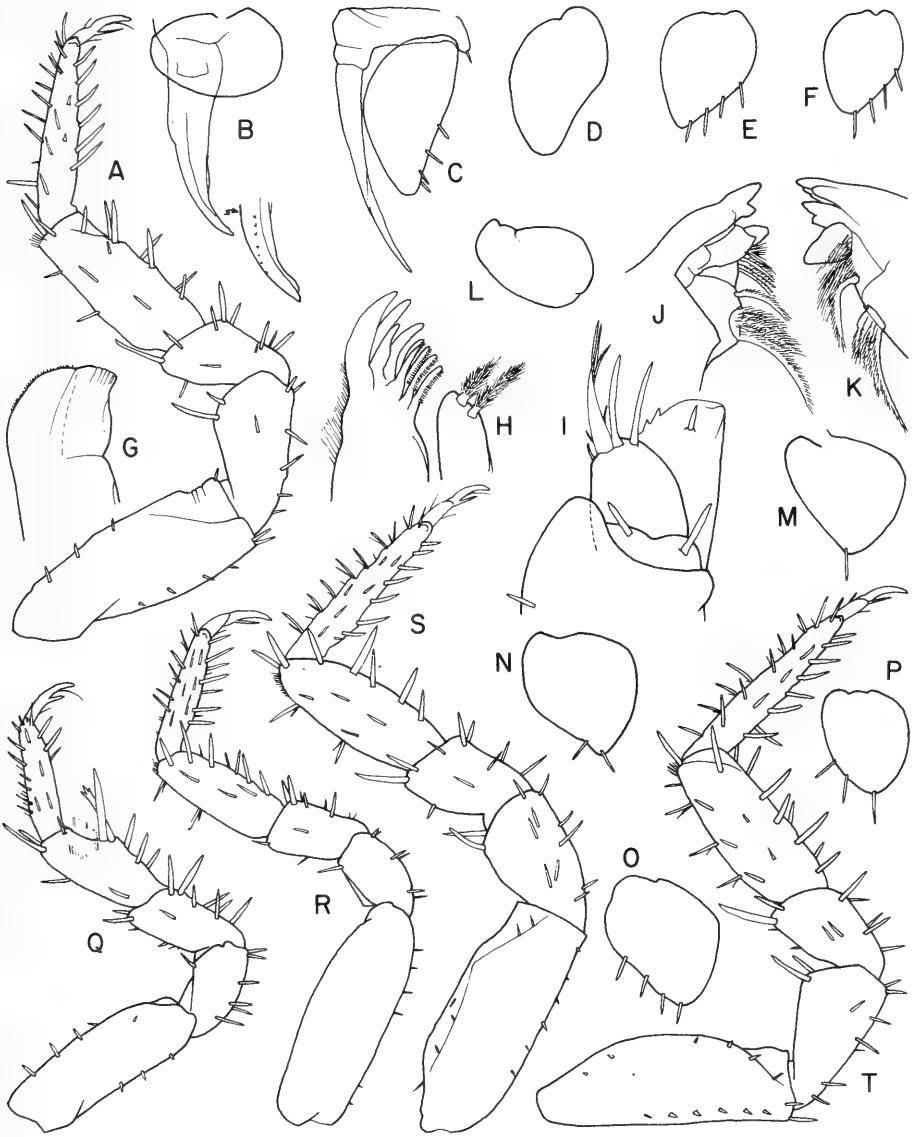


FIG. 4

Alboscia elongata n. gen. n. sp.: A) male pereopod VII; B) male pleopod 1; C) male pleopod 2; D) male pleopod 3; E) male pleopod 4; F) male pleopod 5; G) maxilla 2; H) maxilla 1; I) maxilliped; J) left mandible; K) right mandible; L) female pleopod 1; M) female pleopod 2; N) female pleopod 3; O) female pleopod 4; P) female pleopod 5; Q) female pereopod I; R) female pereopod II; S) female pereopod VI; T) female pereopod VII.

Type locality and distribution. "Paraguay" only.

Deposition of type. The American Museum of Natural History

Balloniscus sellowi (Brandt, 1833)

Type locality and distribution. Montevideo, Uruguay.

Other locations: Argentina, western Brazil and Paraguay ("Rio Apa, Haut Paraguay")

Deposition of types. Types unknown. Others: MNRJ

For detailed descriptions, bibliography and other information on the two species not represented in the present collection see VERHOEFF (1951) and ARCANGELI (1958) and LEMOS DE CASTRO (1958, 1976).

DUBIONISCIDAE n. fam.

The new family is established for *Dubioniscus* Vandel (1963) the type species of which is based on specimens collected from a tropical forest near the Rio de la Plata, Argentina.

Dubioniscidae is characterized by:

Length of oval-oblong body from tiny to small, rarely more than 6 mm long

Antenna 1 with few aesthetascs

Antenna 2 with three flagellar articles

Ocellus or ocelli present

Anterolateral lobes on cephalon well defined

Cephalon sometimes with central-frontal depression into dorsum between two lateral ridges

Molar of mandibles compound

Maxilla 1 exopod with eight mostly plain teeth; endopod without pointed apex

Dorsum smooth covered with tiny scales

Body lightly or moderately pigmented, some in striking pattern (some might be pigmentless)

Pereopod I of male and female (and sometimes II of male) with grooming organ on propodus and carpus

Pleon as broad or about as broad as pereon

Neopleurons on pleons 3 to 5 well defined dorsally, reach to general body margin; sometimes slightly recurved

Exopods of pleopods 1 to 5 of males and females of same general pattern

Pseudotracheae absent

Exopod of uropod extends well beyond tip of pleotelson. Since the morphology of the mouth parts of the species included in *Calycuoniscus* and most species of *Novamundoniscus* are not well known, it would be presumptuous to add definite criteria on mouth parts to the family characters other than to show those characters as illustrated for the species of *Dubioniscus* described here. For the species of the type and sometimes the new genus, flagellar article number is obscure and often mis-

takenly recorded because the division between articles 2 and 3 lacks a clear furrow. Separation of the articles is confirmed (especially in small specimens) when the flagellum is back lighted and viewed in a compound microscope. Rarely have the lateral nodes or glands on the pereons of such small specimens ever been described so that their absence, presence or pattern cannot serve as definitive family, genus or species characters at this time.

TYPE GENUS. *Dubioniscus* Vandel, 1963

OTHER GENERA. A brief synonymy of genera included in Dubioniscidae n. fam. is as follows:

Calycuoniscus Collinge, 1915:509

Dubioniscus Vandel, 1963:78 (= *Hileioniscus* Lemos de Castro, 1967:317,

LEMONS DE CASTRO 1968:407)

Novamundoniscus n. gen. (New World *Phalloniscus* species)

?*Phalloniscus* Budde-Lund, 1908:296 (Old World species)

The species in *Calycuoniscus*, *Dubioniscus* and *Novamundoniscus* n. gen. generally are small rarely over 6 mm long. They have in common dorsal scales, three flagellar articles, well developed neopleurons on segments 3 to 5 and lack of pseudotracheae. The excavate frontal part of the cephalon sets the species of *Dubioniscus* apart from most other species of oniscideans including those in the new genus. Two valid species are included in *Calycuoniscus* and four in *Dubioniscus* (see below).

Calycuoniscus, *Dubioniscus* and *Phalloniscus* have been placed by one worker or another in Oniscidae, Platyarthridae or Bathytropidae. In each family many genera are ill defined, being based on poorly described species. This is especially so for some small to tiny oniscideans. The characters which distinguish species of Dubioniscidae from species of other related families will be discussed in more detail elsewhere. Significant are two flagellar articles in Platyarthridae and Bathytropidae. Oniscidae share three flagellar articles with Calycuoniscidae, but specimens generally are larger and they have the flattened type of pseudotracheae on the exopods of the pleopods. Also, species of Oniscidae rarely have conspicuous scales on the dorsum.

Calycuoniscus Collinge, 1915

COLLIDGE (1915) described *Calycuoniscus bodkini* from Georgetown, Guyana. He recorded the species again in Trinidad when he described a second species, *Calycuoniscus spinosus*, in Guacharo Cave on that island. Neither species were collected in Paraguay. Both species have eyes and pigment and Collinge specifically stated that both species had three flagellar articles in their antennae 2. *Calycuoniscus bodkini* has a peculiar set of hollows in the epistome (see COLLIDGE 1915, plt. 32, fig. 4). *Calycuoniscus spinosus* differs little from *C. bodkini* and it is not recorded to have the peculiar set of hollows in the epistome. LEMOS DE CASTRO (1968:410) recorded *C. bodkini* from Para and Territorio do Amapa, Brazil. Other species have been placed in the genus, but only the two species mentioned here are now in the genus. *Caly-*

cuoniscus goeldii Lemos de Castro (1967) from Brazil is here placed in *Dubioniscus* (see below).

VAN NAME (1936:186) briefly stated for species of *Calycuoniscus* that the division between the ultimate and penultimate articles of the flagellum is "very likely only slightly movable, if at all, thus approaching the two-segmented condition". VANDEL (1963:78) stated that if species of *Calycuoniscus* could be shown to have only two flagellar articles the genus easily could be placed in Bathytropinae (now Bathytropidae). Since all species of *Calycuoniscus* bear three flagellar articles on antenna 2, the genus also cannot be placed in Platyarthridae or Bathytropidae which have two flagellar articles. It has been placed in Oniscidae, but species in that family are large and with flattened pseudotracheae on the endopods of the pleopods.

REMARKS. TAITI & FERRARA (1986:1362), in attempting to clarify the true identity of *Alloniscus compar* Budde-Lund, 1893 from Venezuela, examined the type specimen in the Zoologiske Museum, Copenhagen. They speculated that it might be a species of *Calycuoniscus*. VANDEL (1952a:112) gave a description of *A. compar* on specimens from Venezuela now placed in *Littorophiloscia*. The identity of *A. compar* is uncertain until the type material is reexamined.

Dubioniscus Vandel, 1963

Hileioniscus Lemos de Castro, 1967:317.

Dubioniscus Vandel, 1963b: 2697 (nomen nudum).

Dubioniscus Vandel, 1963:78; 1972a:40. Lemos de Castro, 1968:408; 1970b:1. Vandel, 1973:158; 1981:43.

The type of the genus is *Dubioniscus delamarei* Vandel (1963:78) and it is described below. The division between articles 2 and 3 sometimes is difficult to see in specimens of the type species. VANDEL and LEMOS DE CASTRO erroneously recorded the number of flagellar articles as two. VANDEL stated that, aside from flagellar article number, the peculiar shape of the cephalon set *Dubioniscus* apart from other genera of Bathytropinae. Since the description of *Dubioniscus delamarei* resembled the specimens collected in Paraguay in every morphological character except in flagellar article number, VANDEL's (1963:78) description was reevaluated.

The shape of the apical of two articles as illustrated by VANDEL is the same as that illustrated for articles 2 and 3 here. The division between articles 2 and 3 is visible when antenna 2 from specimens from Paraguay is placed on slide and viewed back lighted in a compound microscope. In addition to resemblances in body type, cephalon type, scales, anterolateral lobes, neopleuron lengths and shapes, pleotelson shape and general form of male pleopods 1 and 2, the pattern of body pigmentation matches almost exactly so there is no doubt that the specimens described here are conspecific with it. LEMOS DE CASTRO (1970b:1) essentially repeated Vandel's account of *Dubioniscus* and included new localities in Brazil. He also described *D. marmoratus* from Brazil.

DIAGNOSIS. Eyes large. Three flagellar articles. Frontal margin of cephalon broadly rounded or excuvate according to angle. Anterolateral lobes of cephalon

conspicuous. Mediofrontal ("frontomedial crush") excuvation in dorsum of cephalon (easily seen in dorsal oblique view). Dorsum covered with tiny scales. Male and female pereopods I with grooming organ. Pleon as wide as pereon with neopleurons 3 to 5 well developed. Pseudotracheae absent. Posterior margin of pleotelson obtusely pointed. Uropod short with short endopod arising anterior to long exopod; both rami project slightly beyond tip of pleotelson.

TYPE SPECIES. *Dubioniscus delamarei* Vandel, 1963. Type by monotypy.
Gender. Masculine.

OTHER SPECIES. *Dubioniscus* Vandel (1963) contains four species some of which might be synonymized when details of each are known. They are:

Dubioniscus delamarei (Vandel, 1963) - Argentina, Paraguay

Dubioniscus goeldii (Lemos de Castro, 1967) n. comb. - Brazil

Dubioniscus marmoratus (Lemos de Castro, 1970b) - Brazil

Dubioniscus negreai (Vandel, 1973b) - Cuba

In his original description of what now is *Dubioniscus goeldii*, LEMOS DE CASTRO (1967) stated that two flagellar articles were present and he placed his monotypic genus *Hileioniscus* in Bathytropidae. He later (1968) illustrated the species and placed it in *Calycuoniscus* because he discovered that there were three flagellar articles. With three flagellar articles, large anterolateral lobes and with the general shape of the cephalon, among other characters, the species really is in *Dubioniscus*, not *Calycuoniscus*. VANDEL (1972) described *Dubioniscus insularis* (= *nomen nudum*) as being from Cuba, however, in his work on oniscideans from Cuba VANDEL (1973b) mentioned only *Dubioniscus negreai* (corrected from *negrae* in VANDEL, 1981).

TAXONOMIC REMARKS. *Dubioniscus* is related to *Calycuoniscus* and *Novamundoniscus* n. gen. When specimens of *Dubioniscus* are reencountered they must be reexamined and the status of each species determined based on knowledge of more details.

***Dubioniscus delamarei* Vandel, 1963**

Figs 5A-N, 6A-N and 7A-D

Dubioniscus delamarei Vandel, 1963:78, Figs 9-11. Lemos de Castro, 1970b:2.

DIAGNOSIS. Shape of exopods of male pleopods unique. Posterior margin of pleotelson produced and obtusely rounded.

DESCRIPTION. About 16 distinct ocelli. Body about 2.5 times as long as broad. Dorsum smooth, covered with tiny scales especially apparent on margins of pereons, pleonal segments and pleotelson. Cephalon shallowly set into pereon I. Cephalon with broad medial depression into dorsum. Frontal line well developed laterally with medial interruption. Frontal margin (dorsal view) broadly rounded. Anterolateral lobes well developed. (If cephalon is tipped forward and downward enough, medial depression clearly is visible centrally on cephalon).

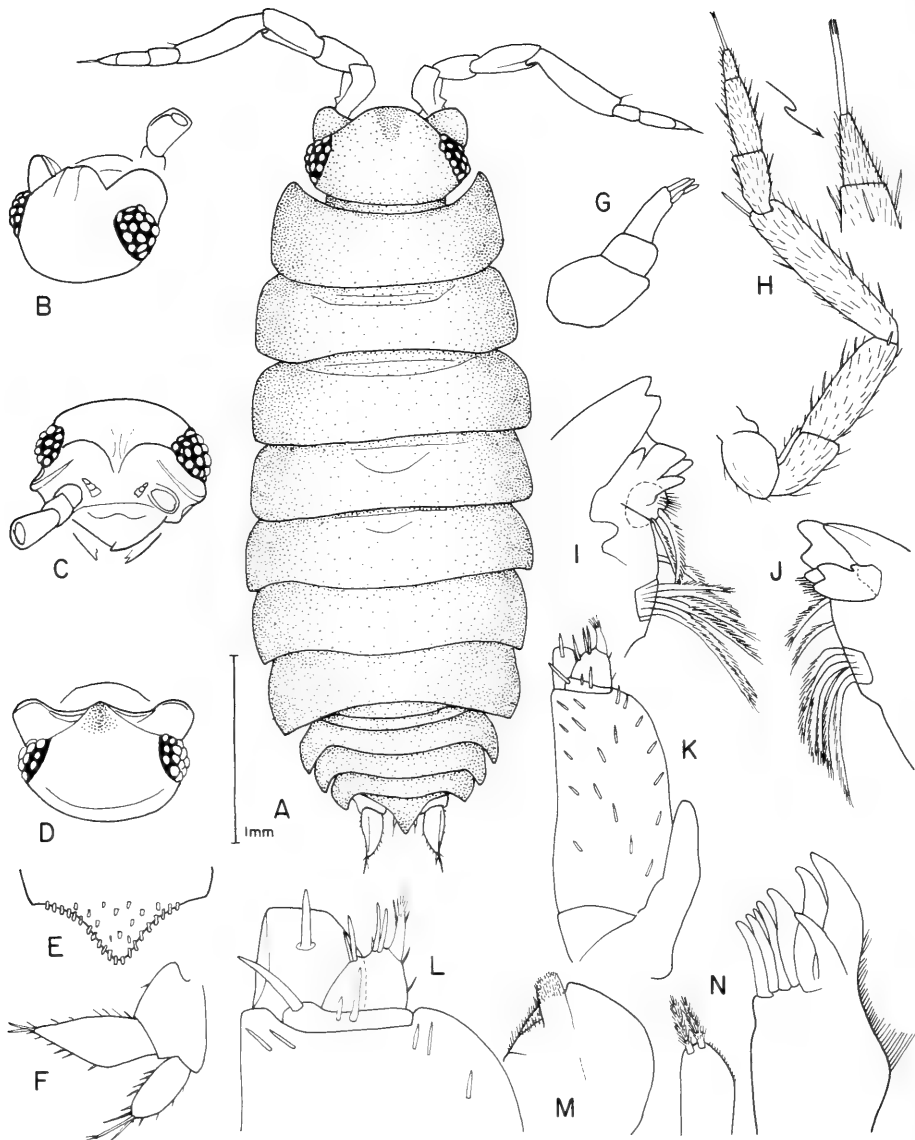


FIG. 5

Dubioniscus delamarei Vandel, 1963: A) dorsal view; B) cephalon, dorsal oblique; C) cephalon, frontal view; D) cephalon, dorsal view; E) pleotelson; F) uropod; G) antenna 1; H) antenna 2 (with detail of flagellar tip); I) left mandible; J) right mandible; K) maxilliped; L) detail maxilliped; M) maxilla 2; N) maxilla 1.

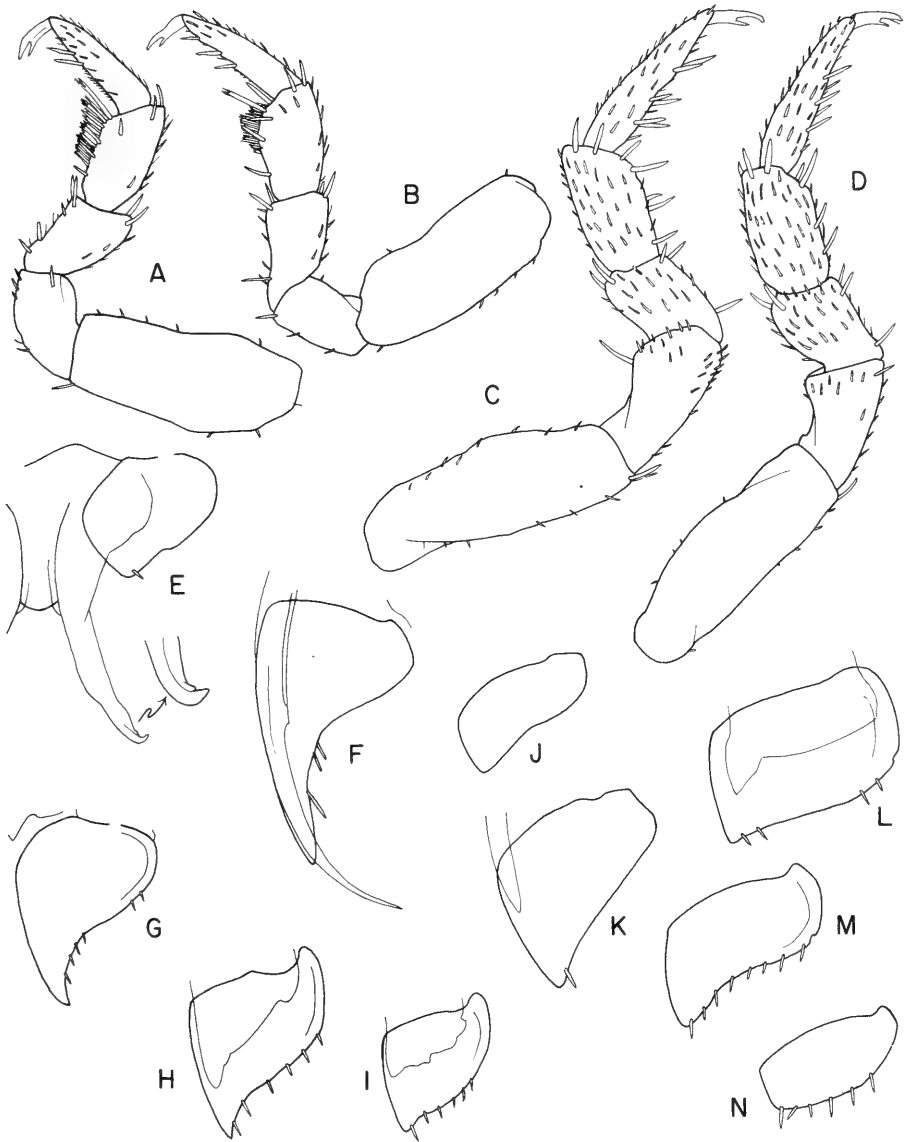


FIG. 6

Dubioniscus delamarei Vandel, 1963: A) male pereopod I; B) male pereopod II; C) male pereopod VI; D) male pereopod VII; E) male pleopod 1; F) male pleopod 2; G) male pleopod 3; H) male pleopod 4; I) male pleopod 5; J) female pleopod 1; K) female pleopod 2; L) female pleopod 3; M) female pleopod 4; N) female pleopod 5.

Antenna 2 moderately long, extending back to about posterior margin of pereon III; flagellar article 2 longest of three articles; apical article shortest, tipped with compound seta. Labrum rounded. Left mandible with compound molar one seta in setal row and two setae on lacinia mobilis. Right mandible with compound molar, one seta in setal row and one on lacinia mobilis. Maxilla 1 with exopod tipped with eight plain teeth; endopod with two penicillate setae near to rounded tip. Maxilla 2 with narrow sensory bulb medially placed on square apex. Maxilliped with scattered long setae on outer surface; blade with one large seta on outer surface and none on sensory edge. Palp of maxilliped with three (two large) setae on segment 1, two setal groups of two setae each on inner margin of segment 2 and apical segment tipped with tuft of setae. Epipod less than half length of maxilliped proper, rounded apically.

Lateral margins of pereon convex. Lateral nodes and glands not apparent. Pereon I partially envelops cephalon and pereon VII with long posterolateral extensions. Pereopods without conspicuous dactylar organ. Male and female pereopods I shortest, each with well defined grooming organ. Male pereopod I with two large setae in inner surface of propodus with bed of short setae as part of grooming organ. Carpus of I with very large sensory seta projecting from brush of similar setae on inner surface; some large setae distally placed laterally and on outer surfaces of carpus; merus with large setae distally placed both on inner and outer surfaces; ischium and basis with few setae. Female pereopod I with two long setae on inner surface with short setae as part of grooming organ; carpus with at least six large setae on inner surface and one distally on outer surface.

Pleon continuous with pereon; segments 1 and 2 with edges under posterolateral extensions of pereon VII; neopleurons on segments 3 to 5 long, broad, recurved and extended to general body margin. Genital apophysis broad with rounded apex. Male pleopod 1 with short exopod, with one marginal subapical seta; endopod with hook shaped apex. Male pleopod 2 with exopod elongate with three long marginal setae; endopod elongate and pointed; pleopod 3 elongate with at least six marginal setae. Exopod female pleopod 1 tiny without marginal setae; pleopod 2 larger than 1 with one subapical seta; exopod pleopod 3 largest with at least four marginal setae. Pleotelson medially produced, apex pointed; fringing and tiny surface setae apparent. Uropod extends beyond tip of pleotelson with basis small; each ramus flattened with exopod arising on an angle to endopod. Both emerge from about same level. Flattened endopod ovate about half length of flattened basis; both rami tipped with few setae.

Particular pattern of brownish red pigment on dorsum and two spots of pigment on outer basis of pereopods. Mature specimens markedly darker than immature. Two very dark outstanding spots laterally placed dorsally on pereon IV and two on posterior border of VII. Spots continue to edges of pleonal segments (see Vandel, 1963:79, Fig. 9).

Measurements. To 4.8 mm long.

TYPE LOCALITY. Punta Lara, north of La Plata, at the edge of Rio de la Plata, Argentina. VANDEL stated that the location was a fragment of a tropical forest.

DISTRIBUTION. The range of the species is extended from northern Argentina and Brazil to Paraguay where it was collected at two stations: Misiones prov., 30 km S San Juan Bautista

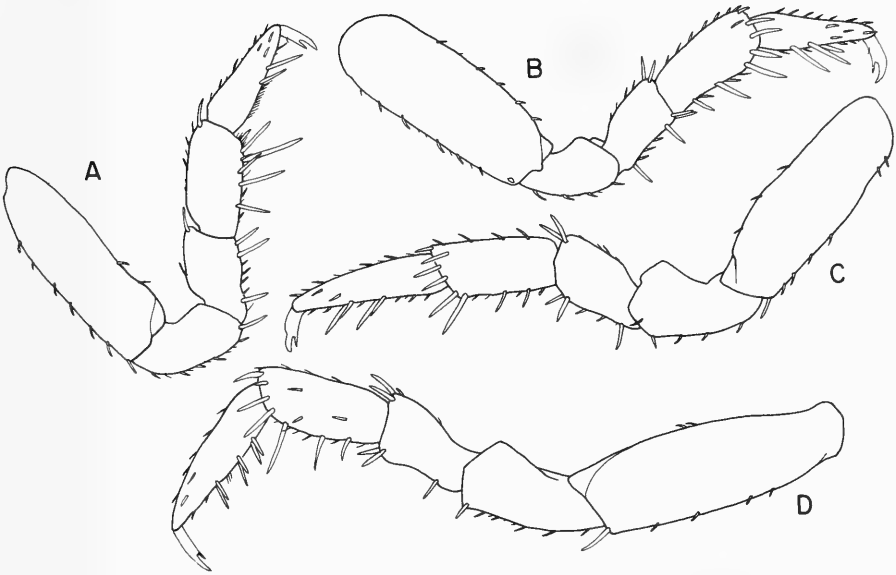


FIG. 7

Dubioniscus delamarei Vandel, 1963: A) female pereopod I; B) female pereopod II; C) female pereopod VI; D) female pereopod VII.

(road to San Ignacio), sifting leaf litter in forest near Ao. Aguaray, 14.X.1982: 1 male, 1 female; Neembucu prov., 5 km NW Pilar, sifting under shrubs (with Cactacea) near Rio Paraguay, 18.X.1982: 8 males, 11 females.

ECOLOGY. The species lives in the leaf litter of forested places. A large female 4.5 mm long had six advanced embryos tightly packed in its marsupium. The largest female was 4.8 mm long.

Deposition of type and other specimens. Type: Unknown. MHNG.

TAXONOMIC REMARKS. *Dubioniscus delamarei* is best compared to *D. goeldii* and *D. bodkini* which have a long broadly rounded pleotelson (see LEMOS DE CASTRO, 1968:409, Figs 1-16). Exopods of male pleopods 1 and 2 are differently shaped as well.

REMARKS. COLLINGE (1915; 1917) stated in his descriptions of two species of *Calycuoniscus* that there were three articles on antenna 2. VANDEL (1963) stated "les plus remarquables du céphalon du *Dubioniscus* réside dans l'existence de lobes frontaux latéraux bien développés, mais ne continuant pas la ligne frontale." It is this character and the three flagellar articles, among others, which defines *Dubioniscus*. Specimens from Paraguay compared perfectly to the specimen illustrated by VANDEL (1963:74, Figs 9-11) in shape of male pleopods 1 and 2 and in dorsal color pattern.

Novamundoniscus n. gen.

pars Phalloniscus Budde-Lund, 1908:296 (New World species only).

Phalloniscus has been a dumping place for many small oniscideans from many diverse temperate and tropical parts of the world. To date about 36 species have been included in the genus. How many of them are valid members is yet to be determined. Species from the New World included in *Phalloniscus* are placed in *Novamundoniscus* n. gen. here. However, more details on the morphology of some species must be made available to confirm their placement in the new genus. In spite of several redefinitions of *Phalloniscus* and placement of about 36 species in it, no accurate definition of the genus or its type species *Oniscus punctatus* Thompson (from Dunedin, South Island, New Zealand) is available (BUDE-LUND, 1908; BOWLEY, 1935; VANDEL, 1952a, b, 1962a, 1973a, 1977).

A brief review of the characters on which many species in *Phalloniscus* are based shows that the genus is composed of a heterogenous assemblage of species many of which are not well defined. Few species really have been compared in particular characters or in detail to the type or related species from New Zealand. Species of *Phalloniscus* from the Old World (including New Zealand) and species from the New World are in many important characters markedly different. VANDEL (1962a:531) stated that someday isopodists might take all species of *Phalloniscus* and "... il soit amené à les ranger dans des genres distincts." Each species must be redescribed and reevaluated so that *Phalloniscus* itself can be redefined accurately. Descriptions of all former species of *Phalloniscus* from the New World were examined and the following tentative diagnosis of *Novamundoniscus* resulted.

DIAGNOSIS. Eyed (or eyeless). Three flagellar articles. Anterolateral lobes moderately well developed; frontal line interrupted medially. Dorsum lightly covered with scales. Glands and lateral nodes, if present, not at all well defined. Pigmentation of dorsum various (sometimes absent?). Molar of mandible compound. Maxilla 1 exopod tipped with regular and bifurcate teeth. Maxilla 2 with distinct sensory bulb mediolaterally placed on tip. Apical article on maxilliped tipped with distinct setae not tuft of setae; distinct setae in two groups on inner margin of second palp article; basal article with at least two long setae. Endite or blade of maxilliped simple with one seta. Pleon as wide as pereon, with neopleurons well developed on segments 3 to 5. Pereopod I of male with grooming organ. Pseudotracheae absent. Exopod of male pleopod 1 about 1/3 length of simple with no marginal setae; endopod acutely pointed. Exopods of pleopods 2 to 5 with few to several setae on margins. Pleotelson broad with posterior margin obtusely rounded. Uropods project well beyond tip of pleotelson. No species of *Phalloniscus* from New Zealand or Europe has this combination of characters.

TYPE SPECIES. *Phalloniscus vandeli* Lemos de Castro, 1959. Type by original designation.

Gender. Masculine.

OTHER SPECIES. The 12 named species formerly in *Phalloniscus* from the New World are tentatively transferred to *Novamundoniscus* n. gen.:

Phalloniscus avrilensis (Van Name, 1940)
Phalloniscus baldoni (Arcangeli, 1930)
Phalloniscus barbouri (Van Name, 1926)
Phalloniscus dissimilis Lemos de Castro, 1959*
Phalloniscus langi Van Name, 1936
Phalloniscus macrophthalmus Lemos de Castro, 1959*
Phalloniscus marcuzzii Vandel, 1952a*
Phalloniscus pearsei Van Name, 1936
Phalloniscus persimilis Vandel, 1952a*
Phalloniscus setosus Lemos de Castro, 1959
Phalloniscus singularis Lemos de Castro, 1967*
Phalloniscus sp. Lenko, 1966
Phalloniscus vandeli Lemos de Castro, 1959*

Only *Phalloniscus macrophthalmus* and species marked with an "*" should be thought to be included with some assurance in *Novamundoniscus* n. gen. based on knowledge of relevant characters. Complementary information was added to the description of *P. singularis* by LEMOS DE CASTRO (1970a).

REMARKS. Enough differences are present to separate species from the New World from those recorded from New Zealand and Europe. *Novamundoniscus* n. gen. is the first set of species to be removed from the former about 36 species of *Phalloniscus*.

Novamundoniscus vandeli (Lemos de Castro, 1959) n. comb. Figs 8A-M and 9A-Q

Phalloniscus vandeli Lemos de Castro, 1959:205, Pl. I, Figs 1-9.

DIAGNOSIS. Shape of male pleopods 1 and 2 diagnostic.

DESCRIPTION. Darkly pigmented eyes of 8 to 11 ocelli. Body about 2.4 times as long as broad. Dorsum lightly covered with tiny scales; very light redish brown to dark brown pigment (largest specimens darkest). Cephalon set moderately deep into pereon I. Cephalon with obtusely rounded frontal margin; anterolateral lobes small and inconspicuous. Frontal line present only laterally with a small medial bulge arising from front of cephalon. Supra-antennal line defined only over antennae 2. Lateral nodes present. Glands, if present, not well defined. Antenna 1 with six aesthetascs three each in two tiers. Antenna 2 extends back to about posterior edge of pereon III; flagellum shorter than peduncular segment 5 with three subequal articles apical one tipped with compound seta. Joint between flagellar articles 2 and 3 (unless backlighted) appears to be fused (the two articles can appear to be one article).

Labrum broadly rounded with some sensory setae medially on edge. Right mandible with compound molar; two setae in setal row; one on lacinia mobilis. Left mandible with compound molar; one seta in setal row; one on lacinia mobilis. Hypopharynx bilobed with scale-like seta on apex of each lobe. Maxilla 1 with three large and one small plain teeth on outer apical margin; four, one bifurcate, smaller teeth on inner apex; endopod with two apical penicillate setae. Maxilla 2 with broad

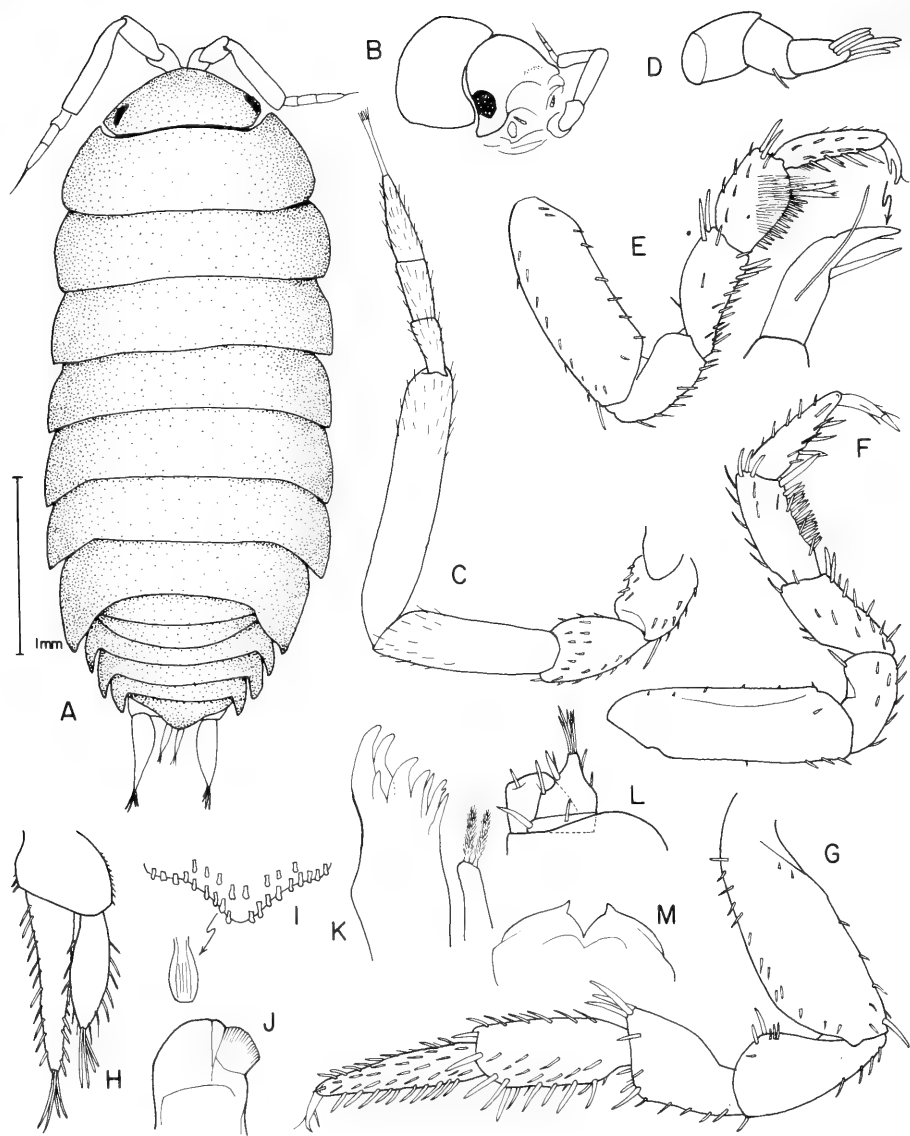


FIG. 8

Novamundoniscus n. gen. *vandeli* (Lemos de Castro, 1959): A) dorsal view; B) cephalon, oblique view; C) antenna 2; D) antenna 1; E) male pereopod I; F) male pereopod II; G) male pereopod VII; H) uropod; I) pleotelson, with detail of scales; J) maxilla 2; K) maxilla 1; L) maxilliped; M) hypopharynx.

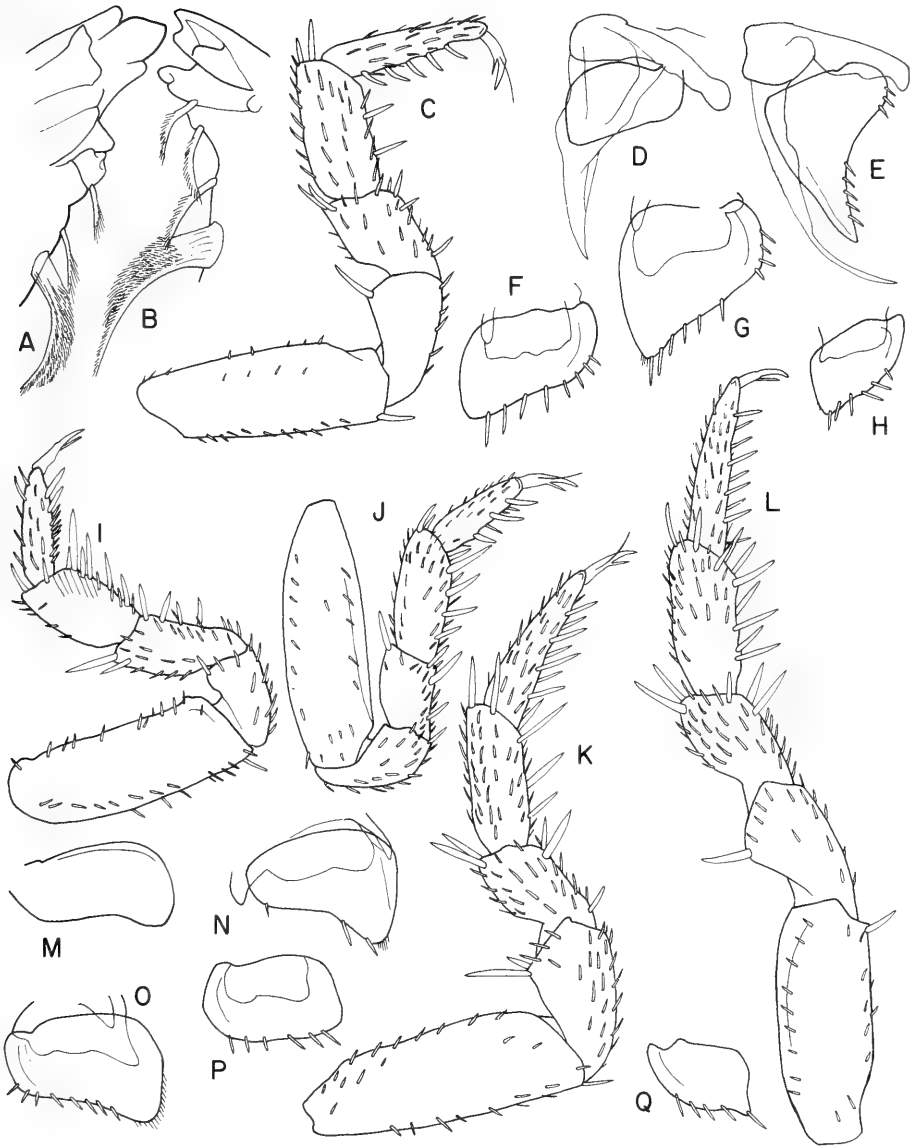


FIG. 9

Novamundoniscus n. gen. *vandeli* (Lemos de Castro, 1959): A) right mandible; B) left mandible; C) male pereopod VI; D) male pleopod 1; E) male pleopod 2; F) male pleopod 4; G) male pleopod 3; H) male pleopod 5; I) female pereopod I; J) female pereopod II; K) female pereopod VI; L) female pereopod VII; M) female pleopod 1; N) female pleopod 2; O) female pleopod 3; P) female pleopod 4; Q) female pleopod 5.

sensory bulb on inner third of rounded apex. Maxilliped with outer surface with many scale-like setae; blade tipped with one seta on inner margin near plain sensory edge. Palp with two long setae on basal segment; second segment with two large setae, each with smaller seta arising from upper part of inner rounded margin; apical segment tipped with broad set of long setae. Epipod of maxilliped more than half length of maxilliped proper, apex acutely pointed.

Pereon with lateral margins more or less parallel. All pereopods with simple string-like dactylar organ. Male pereopod I with four setae on inner surface of propodus; carpus with two large sensory setae on inner surface projecting from brush of many shorter sensory setae, long setae apically placed on outer surface. Female pereopod I with two long setae and other setae, but no brush of setae on inner surface of carpus; carpus with one very long seta and other setae on inner surface.

Pleon continuous with pereon; segments 1 and 2 enclosed within curved posterolateral extensions of pereon VII. Elongate neopleurons on segments 3 to 5 slightly recurved, extended to general body outline. Genital apophysis simple. Male pleopod 1 with exopod short and simple; endopod elongate with pointed tip. Male pleopod 2 elongate with at least eight marginal setae; endopod long and thin; pleopods 3 to 5 short with progressively fewer marginal setae on each. Female pleopod 1 exopod simple; pleopod 2 with produced medial margin with three marginal setae. Female pleopods 3 larger 4 and 5 with progressively less setae on margins. Pleotelson medially produced with rounded apex; marginal and dorsal scales conspicuous. Uropod with short basis projects only slightly from under pleotelson; endopod about 2/3 length of exopod; both rami tipped with few setae.

Measurements. Adult specimens range between 3.5 and 4 mm long.

TYPE LOCALITY. Barra do Sana, Macae, Estado do Rio de Janeiro, Brazil.

DISTRIBUTION. LEMOS DE CASTRO recorded the species from Estado do Minas Gerais and Estado do Rio de Janeiro, Brazil. The species was the most numerous and widespread of all oniscideans collected in Paraguay having been taken at 27 stations which are as follows: Alto Parana prov., near Puerto Santa Teresa, sifting leaf litter in tropical forest, 3.XI.1979: 21 ex.; Ciudad del Este (= Pto Pte Stroessner), Forestry school, sifting litter in primary forest, 6.XI.1979: 2 ex.; same loc., in pin tree forest, 15.II.1983 (Ig. P. Berner): 2 ex.; near Arroyo Itabo Guazu, sifting litter in tropical forest, 4.XI.1979: 14 ex.; Amambay prov., 80 km S Bella Vista, near Ao. Negla, sifting bamboo litter, 1.XI.1979: 4 ex.; Parc Nacional Cerro Cora, sifting leaf litter, 24.X.1979: 7 ex.; Caaguazu rov., 20 km N Colonel Oviedo, sifting leaf litter in forest, 7.X.1979: 6 ex.; Canendiyu prov., Rio Carapa near junction with Rio Alto Parana, sifting litter in tropical forest; Central prov., San Lorenzo, Villa del Maestro, sifting leaf litter, 5.X.1979: 25 ex.; Colonia Thompson, 20 km S Asuncion, sifting leaf litter and rotten wood, 10.XI.1979: 14 ex.; Concepcion prov., Colonia Sgo Jose E. Lopez, sifting in forest islands, 13.X.1979: 14 ex.; Estancia Estrellas, banks of Rio Apa (50 km E San Lazaro), sifting in gallery forest, 15.X.1979: 2 ex.; between Est. Estrellas and Est. Primavera, sifting in dry forest, 16.X.1979: 27 ex.; Est. Viancho Postillon (5 km E Puerto Max), sifting in gallery forest, 19.X.1979: 54 ex.; between Isla Real and Est. Sta Maria, sifting in gallery forest of Ao. Tagatya - mi, 20.X.1979: 62 ex.; near Estancia Garay-Cue, sifting bamboo litter, 22.X.1979: 8 ex.; same loc., sifting in dry forest, 22.X.1979: 1 ex.; Itapua prov., 10 km S Santa Maria, sifting in primary forest, 25.X.1982: 19 ex.; San Benito (Pastorea), sifting in gallery forest with bamboos, 29.X.1982: 8 ex.; 4 km above Salto Tembey, sifting litter in tropical forest, 1.XI.1982: 9 ex.; Misiones prov., 30 km S San Juan Bautista (road to San Ignacio), near crossing over Ao. Aguary, sifting forest litter, 14.X.1979: many (specimens redescribed); Panchito Lopes (4 km N Yabebyry), sifting of forest litter, 22.X.1982: 23 ex.; Neembucu prov., 5 km NW Pilar,

sifting under shrubs (with Cactacea) near Rio Paraguay, 18.X.1982: many; same loc., sifting in Eucalyptus plantation, 18.X.1982: 20 ex.; Paraguari prov., 3 km N Carapegua, sifting under shrubs, 7.X.1982: many.

ECOLOGY. The species is widespread in Paraguay where it lives in moderately moist leaf litter and organic detritus.

Deposition of type and other specimens. Types: MNRJ. Others: USNM 267280. BM(NH) 1994.4797-4806. MHNG.

TAXONOMIC REMARKS. The specimens described here also closely correspond in morphology to *Novamundoniscus macrophthalmus* also collected from near Rio de Janeiro by LEMOS DE CASTRO (1959:205). The specimens described here correspond most closely to the description and illustrations of *N. vandeli* in cephalon type and overall eye size (not in ocelli number). They correspond in many other details to the illustrations of *N. macrophthalmus*, although most characters are intermediate. The number of ocelli in *N. vandeli* is about eight and in *N. macrophthalmus* it is about 13. The eye as a whole on the specimens described here (8 to 11 ocelli) does not appear to be as large as those illustrated for *N. macrophthalmus*. Specimens of *N. vandeli* less than 2 mm long have only five ocelli suggesting that ocelli number increases with molt. After determining the number of ocelli in mature specimens from several locations, the number tends to be closer to eight and this makes the specimens collected here closer to *N. vandeli* rather than to *N. macrophthalma* with 13 ocelli.

The shape of the exopod of male pleopod 1 is intermediate in shape between the simple shapes of both species. The species *N. vandeli* has less than the four bifurcate teeth on the tip of the exopod of maxilla 1. Only one was seen clearly on maxilla 1 of the specimen illustrated here. *N. setosus* also is very similar to the former species. *N. dissimilis* has a differently shaped exopod of male pleopod 1 and the tip of the endopod has a unique shape. Examination of a series of specimens from southern Brazil and Paraguay might show a gradation of characters which would show that *N. vandeli*, *N. macrophthalmus* and *N. setosus* are conspecific. *N. dissimilis* most likely will remain as a distinct species.

REMARKS. Short, young specimens of *N. vandeli* differ enough from adult specimens to be mistaken as a different species. The ocelli number for specimens of 2 mm or less is five. The short specimens have a lighter body pigment and a superficial "frosted" appearance when compared to adults. A gradual darkening of color is correlated with length. The frosted appearance is, in part at least, the result of the presence of many tiny scales on the dorsum which probably are proportionately larger on young specimens than on adults.

PLATYARTHRIIDAE

Species of Platyarthridae are with or without ocelli. They are small, covered with tiny scales, with two flagellar articles and they lack pseudotracheae. The pereon-pleon width and shape of the neopleurons vary according to species. The posterior margin of the pleotelson either is obtusely pointed or broadly rounded. Uropods are

elongate but of many shapes. Pigmentless, lightly pigmented and darkly pigmented species are known. Ocelli number and body pigmentation are correlated and those with no pigment rarely have an ocellus or they have only one or a few ocelli. Platyarthrids, especially species in *Trichorhina*, frequently are collected in leaf litter and thick organic decay. Species are from tropical and warm temperate regions in the world and several are expansive, having been spread throughout much of the warmer parts of the world by humans. *Trichorhina heterophthalma* recorded here is such a species.

Some species of Platyarthridae are parthenogenetic. Many species of Platyarthridae are associated with ants. The two species of Platyarthridae recorded here from Paraguay, one without ocelli (*Trichorhina brasiliensis*) and one with two ocelli (*T. heterophthalma*), are not directly associated with any particular ant or other insect hosts. Males and females are known for both species. VANDEL (1962a:433) included a comprehensive definition of Platyarthridae (= Squamiferidae) and he included an extended definition of *Platyarthrus* (p. 441) and *Trichorhina* (p. 434). Characters on which many species in several genera of Platyarthridae can be distinguished with confidence are yet to be established.

Trichorhina Budde-Lund, 1908

DIAGNOSIS. Eyed or without eyes. Two flagellar articles. Frontal line and supra-antennal lines not easily distinguished. Body oblong-oval, pigmentless or lightly pigmented; dorsum covered with tiny scales. Pereon-pleon width variable. Shape and length of neopleurons variable. Pseudotracheae absent. Uropods reach beyond tip of pleotelson. Posterior margin of pleotelson pointed or obtusely rounded.

TYPE SPECIES. *Alloniscus tomentosus* Budde-Lund, 1893 (= *Trichorhina tomentosa*).

Gender. Feminine.

OTHER SPECIES. About 65 species worldwide have been included in *Trichorhina*. Most are poorly described so many must be redescribed to be confirmed as a member of the genus or to determine actual taxonomic placement.

REMARKS. VANDEL (1952b:526) described *Phalloniscus bolivianus* from one female specimen 4.5 mm long taken in Bolivia. Antennae 2 were missing from the specimen. He placed the species in *Phalloniscus* because the pattern of glands and pores on the pereons were more like those in Oniscidae rather than those in his Squamiferidae (= Platyarthridae). Six ocelli were recorded. Pseudotracheae were absent. Later VANDEL (1956:300) described the male and showed that it had two, not three, flagellar articles. He then placed *Phalloniscus bolivianus* in *Trichorhina* because of the two flagellar articles and lack of pseudotracheae among other characters.

Trichorhina heterophthalma, a cosmopolitan species (see above) distinguished by the presence of two ocelli, is recorded here for the first time from Paraguay (see SOUZA-KURY, 1993). One gravid female specimen 2.5 mm long was taken at Concepcion near Estancia Garay-Cue, sifting bamboo litter, 22.X.1979. Lack of ocelli

makes *T. brasiliensis* (redescribed below) different from *T. heterophthalma* (2 ocelli) and from *T. boliviana* (6 ocelli) collected in nearby Bolivia. Two new species recorded from Brazil by SOUZA-KURY (1993) have eyes.

Trichorhina brasiliensis Andersson, 1960

Figs 10A-O and 11A-R

Trichorhina brasiliensis Andersson, 1960:552, fig. 8.

The pigmentless species without eyes was described by ANDERSSON (1960) from Nova Teutonia, Ita, Estado do Santa Catarina, Brazil. His description was based on a tiny male 1.82 mm long and one tiny female. Here both male and female are described in detail, based on mature specimens. Only minor differences are present when compared to Andersson's less comprehensive description.

DIAGNOSIS. Eyeless. Oblong-oval body pigmentless. Anterolateral lobes small. Pleon about as wide as pereon. Male pleopod 1 with exopod short and simple; endopod elongate, only moderately curved apically. Male pleopod 2 exopod produced with two large subapical setae; endopod long, thin and pointed.

DESCRIPTION. Eyeless. Oblong-oval body about two times as long as broad, pigmentless (cream colored). Dorsum with tiny scales covering relatively thin, shiny integument. Cephalon slightly more than half width of pereon I into which it is set. Anterolateral lobes small. Frontal margin of cephalon rounded (dorsal view). Antenna 1 with at least six aesthetascs bunched apically. Antenna 2 short not extending beyond posterior border of pereon III. Flagellum with two articles about as long as peduncular article 5 with article 1 about half length of article 2. Flagellar articles covered with long setae and article 2 tipped with long compound seta; peduncular articles covered with small scales and few setae.

Labrum broadly rounded with some medial small fringing setae. Left mandible with compound molar, one seta in setal row and two setae on lacinia mobilis. Right mandible with compound molar, one seta in setal row and lacinia mobilis without setae. Hypopharynx with two large lobes with seta at apex; one tiny medial lobe. Exopod of maxilla 1 with three large outer plain teeth, three inner teeth, medial one bifurcate; endopod with two subapical penicillate setae. Maxilla 2 with apical, medial 1/3 expanded slightly into medial sensory bulb. Maxilliped with outer surface with few long setae, blade with long seta; basal segment of palp with three setae, medial one shortest; second segment with two setae on curved inner border, first one single, second with several setae; apical segment pointed with long setae. Epipod of maxilliped more than half as long as maxilliped proper, apex rounded.

Pereon with convex lateral borders. All pereopods covered with scale-like setae; tip of dactylus with two claws, upper one curved, lower one thin and sharp. Male pereopod I with two setae on inner surface; grooming modifications confined to propodus; carpus with many setae on inner surface. Shape and setation of female pereopod I resembles that of male; grooming organ absent.

Pleon continuous with pereon with segments 1 and 2 enclosed within convexity of posterior border of pereon VII. Neopleurons on segments 3 to 5 recurved and

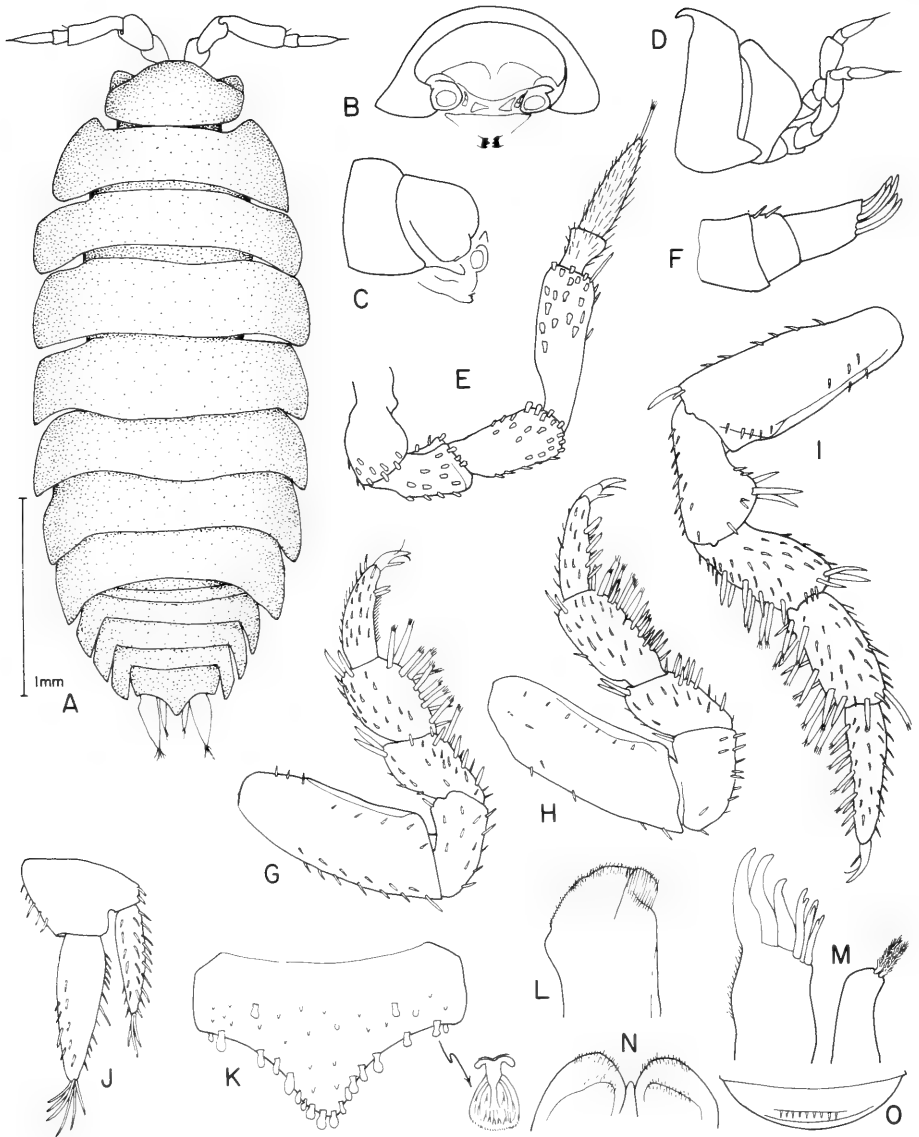


FIG. 10

Trichorhina brasiliensis Andersson, 1960: A) dorsal view; B) cephalon, frontal view; C) cephalon, lateral view; D) cephalon, posterior oblique view; E) antenna 2; F) antenna 1; G) male pereopod I; H) male pereopod II; I) male pereopod VI; J) uropod; K) pleotelson, with detail of scales; L) maxilla 2; M) maxilla 1; N) hypopharynx; O) labrum.

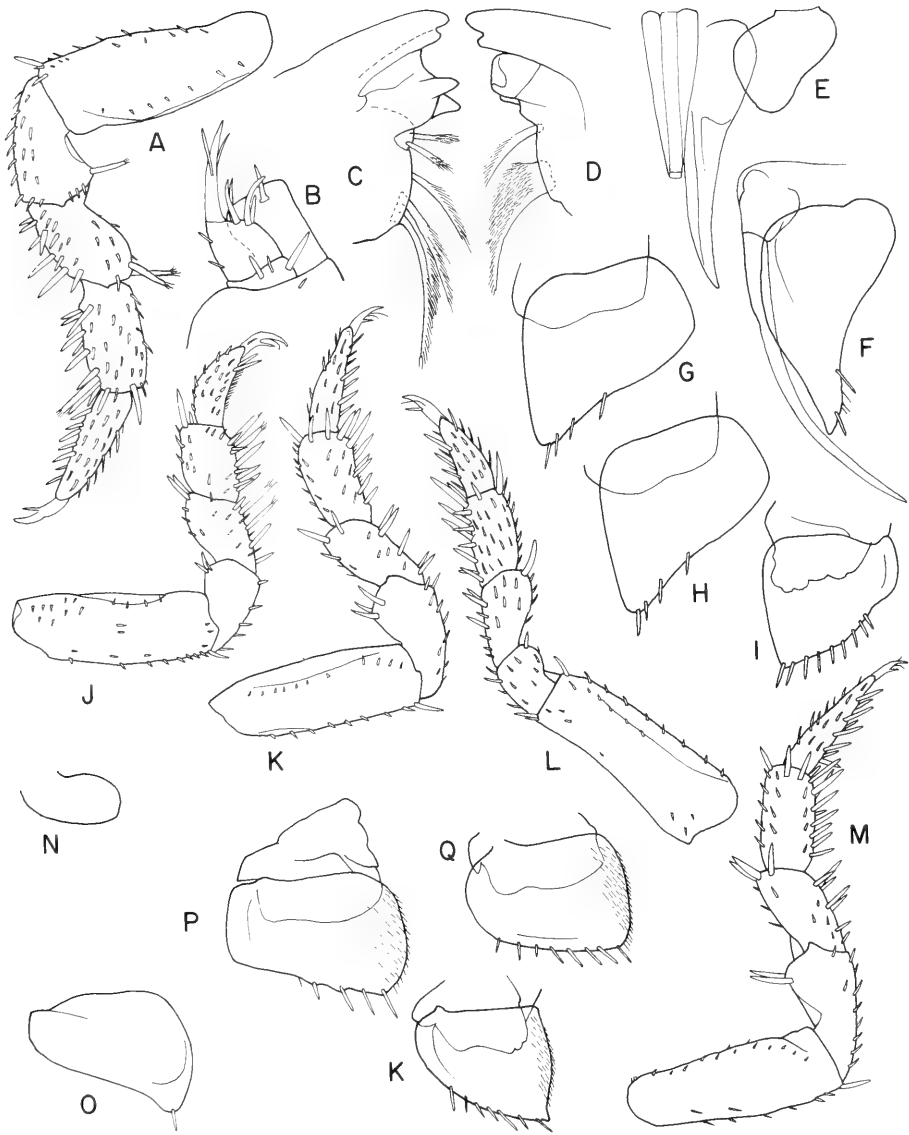


FIG. 11

Trichorhina brasiliensis Andersson, 1960: A) male pereopod VII; B) maxilliped; C) left mandible; D) right mandible; E) male pleopod 1; F) male pleopod 2; G) male pleopod 3; H) male pleopod 4; I) male pleopod 5; J) female pereopod I; K) female pereopod II; L) female pereopod VI; M) female pereopod VII; N) female pleopod 1; O) female pleopod 2; P) female pleopod 3; Q) female pleopod 4; R) female pleopod 5.

extended to general body margin. Genital apophysis simple. Male pleopod 1 with exopod short and simple; endopod elongate, only moderately curved apically. Exopod of male pleopod 2 produced with two large subapically setae; endopod long, thin and pointed. Male pleopods 3 to 5 simple with four fringing setae on 3 and 4 and nine on 5. Female pleopod 1 tiny and rounded; pleopod 2 simple with one apical seta. Female pleopods 3 to 5 simple with four setae on 3, eight on 4 and seven on 5. Pleotelson with posterolateral margins strongly concave, posterior margin medially produced to point. Uropod extends well beyond tip of pleotelson with basis hidden and rami partially hidden (dorsal view); endopod tiny; exopod somewhat stout, length slightly longer than medial length of pleotelson; each rami tipped with setae.

Measurements. Holotype male 3.3 mm long; other specimens range between 3.5 and 4 mm long.

TYPE LOCALITY. Nova Teutonia, Ita, Estado do Santa Catarina, Brazil.

DISTRIBUTION. The species was collected at five stations: Canendiyu prov., N Curuguaty, sifting litter in gallery forest, banks of Rio Jejui-Guazu, 29.X.1979: 1 male, 1 female, the specimens illustrated here are from this station; Concepcion prov., near Estancia San Luis, sifting leaf litter, 15.X.1979: 1 ex.

ECOLOGY. The type specimens were collected from under rocks.

Deposition of type and other specimens. Holotype male and female - Swedish State Museum, Stockholm. MHNG.

TAXONOMIC REMARKS. The species resembles *Trichorhina boliviana* in the general shape of the exopods of male pleopods 1 and 2 and in the configuration and setal pattern of the maxilliped. However, that species clearly has six ocelli. *Trichorhina heterophthalma* (recorded above) has two ocelli and *T. tomentosa*, also a very widespread species, has one ocellus. ANDERSSON (1960:555) compared the species to other species of *Trichorhina* without ocelli. Species of *Trichorhina* without ocelli have been recorded from caves in Mexico, but they are poorly characterized.

SCLEROPACTIDAE

Scleropactidae is based on *Scleropactes*, a genus which has two flagellar articles on antenna 2. Other genera in the family have three flagellar articles. Scleropactids are small to moderately long, with a highly arched body and smooth dorsum. They roll into a tight ball. SCHMALFUSS (1980) reviewed the genera of Scleropactidae (= Sphaeroniscidae) including *Circoniscus*. The family is defined in part on the characteristic shapes of the pleotelson and uropods. Later SCHMALFUSS (1986, Fig. 1) revised his cladogram and included *Circoniscus* and *Sphaeroniscus* as a sister group with notches on the underedge of pereon I as a common character and flagellar article number, two for species of *Circoniscus* and three for species of *Sphaeroniscus*, as a differentiating character.

Circoniscus Pearse, 1917

Circoniscus was based by PEARSE (1917) on *C. gaigei* from British Guiana (now Guyana). The genus was reviewed by SOUZA & LEMOS DE CASTRO (1991) who revived four previous synonyms of the type, *C. gaigei* and described three new species. SOUZA & LEMOS DE CASTRO did not mention *Parcirconiscus ornatus* Verhoeff which was reduced to a synonym of *C. gaigei* by SCHMALFUSS (1986, p. 8). SOUZA & LEMOS DE CASTRO present no reasons why they removed the former species from synonymy with *C. gaigei* and they defined their new species on very unconvincing characters. There probably are only two species in *Circoniscus*, the type *C. gaigei* (with synonyms *C. hamatus* Van Name, *C. intermedius* Souza & Lemos de Castro, *Paracubaris spinosus* Collinge and *Parcirconiscus ornatus* Verhoeff) and *C. bezzii* Arcangeli (with synonyms *C. gracilidens* Souza & Lemos de Castro, *C. incisus* Souza & Lemos de Castro and *C. pallidus* Arcangeli). The two species are separated on differences in the configuration of the underedges of pereons I and II and their ranges of distribution are represented on the map (p. 62) of SOUZA & LEMOS DE CASTRO. The species *C. gaigei* (northern South America and Amazon valley) has only the underedge of pereon I notched and the species *C. bezzii* Arcangeli (northern Rio de la Plata drainage including Paraguay to coast near Rio de Janeiro) has pereon I and II (sometimes III) with a notch. A full synonymy of the genus and its two species now is in preparation.

DIAGNOSIS. Dorsum smooth. Two flagellar articles. Body highly arched, rolls into almost perfect ball with antennae 2 within ball. Epistome well developed projecting shelf-like above frontal line across anterior of cephalon. Underedges of pereon I (and for some species II and III) variously notched. Notch on I always indicated in lateral view. Thin pseudotracheae on exopods of pleopods 1 to 3. Basis of uropods flattened; exopods emerge medially and obliquely from inner edges of bases just beyond tip of broadly rounded pleotelson; endopods project between exopods; tips of both pairs of rami not extending beyond posterior body margin formed by posterior flattened edges of bases.

TYPE SPECIES. *Circoniscus gaigei* Pearse, 1917. Type by monotypy.

DISTRIBUTION. Species of *Circoniscus* are widespread in South America and have been recorded in several locations in Guyana, French Guiana, Brazil, Peru and now Paraguay.

Circoniscus bezzii Arcangeli, 1931

Fig. 12J-M

Circoniscus bezzii Arcangeli, 1931:115, Pl. 2. VAN NAME, 1936:311, Fig. 184. SOUZA & LEMOS DE CASTRO, 1991:50, Figs 23-44.

DESCRIPTION. Paraguay specimens: About 11 ocelli. Notch on underedge of pereons I, II and III. Color brown. For details see SOUZA & LEMOS DE CASTRO (1991, p. 50, Fig. 23-44).

Measurements. 9.6 and 7 mm long.

TYPE LOCALITY. Carandasinho, Brazil (near the border with Bolivia).

DISTRIBUTION. Paraguay. Two nongravid females were collected in Canendiyu prov., 20 km S Salto de Guaira, 1.XI.1979: 2 ex. (sifting litter in primary tropical forest). Brazil. SOUZA & LEMOS DE CASTRO (1991, Fig. 108) recorded the species from sites in the upper Rio de la Plata drainage out to the coast in the Rio de Janeiro region.

ECOLOGY. Leaf litter.

Deposition of type and other specimens. Type: Torino (Arcangeli). Others: MNRJ. MHNG.

TAXONOMIC REMARKS. The female specimens described here were taken within the range of *C. bezzii* and they differ from describes specimens of *Circoniscus gaigei* because they have notches on the underedges of pereons I and II, not just I.

ARMADILLIDAE

Armadillidae are oniscideans which have: Eyes. Thick integument. Dorsum pigmented, smooth or with low tubercles, some with spines. Highly arched body rolls into ball (except Australiodillinae Vandel, 1973) with antennae 2 kept within ball. Two flagellar articles. Five (sometimes four) pairs of pseudotracheae. Underedge of pereon I and sometimes II and III notched for rolling into tight ball for many species. Sometimes with small notch on underside of pereon I (e.g., Cubarinae). Endopod of maxilla 1 always with two penicillate setae. Flattened basis of uropods and hourglass-shaped pleotelson incorporated into expanded neopleurons of pleonal segment 5. Small to tiny exopod of uropod external on flattened basis, endopod long, medially located beneath pleotelson, rarely projecting from below pleotelson (dorsal view). Species of Armadillidae need to be better described and the notches on the underedges of pereons II and III (if present) should be used in addition to the groove on pereon I (if present) to separate genera. The absence or presence and size of the exopod of female pleopod 1 should be recorded since knowledge of its morphology is helpful in diagnosing some genera.

Most species of Armadillidae live in habitats in tropical locations which are wet much of the year, but which dry in the dry season or during some part of the year. Some live in semidesert locations. Armadillids probably live in the driest of all habitats where oniscideans have been recorded. For a good definition and discussion of Armadillidae, see VANDEL (1962a:853).

Two genera of Armadillidae, *Cubaris* and *Venezillo*, are present in Paraguay. *Cubaris* is represented by the type *C. murina* Brandt (1833) which is common in many dry, tropical locations having been widely spread by humans. VAN NAME's (1936) inclusion of *Armadillo borellii* Dollfus (1894) from Rio Apa, Haut Paraguay as a synonym of *C. murina* apparently was accepted by ARCANGELI (1956) who revised *Venezillo*. By comparing the undersides and underedges of pereons I and II species of *Cubaris* and *Venezillo* easily can be told apart. Species of *Cubaris* have a tiny notch on the underside of pereon I and the underedge of the pereon is unmodified (VAN NAME, 1926:389, Fig. 236). The underedges of pereons II and III also are

unmodified. Species of *Venezillo* have a groove of various lengths on the underedge of pereon I (sometimes not well defined) and the underedge of pereon II (and sometimes III) is modified variously with a notch. The notch serves as a "stop" which receives the posterior pereon when specimens roll into a ball.

Venezillo Verhoeff, 1928

VAN NAME (1936), in his summary of oniscideans from the New World, included most species of Armadillidae in *Cubaris*. *Venezillo*, originally a subgenus of *Armadillo*, was raised to genus by ARCANGELI (1956) who reclassified all species of the genus and some species of related genera then known. *Venezillo bolivianus* and a new species are recorded here from Paraguay.

DIAGNOSIS. Rolls into tight ball. Underedge of pereon I modified with groove of various lengths always opening, sometime expanding, at posterior edge (sometimes underedge broad and groove apparently absent). Pereons II and sometimes III with underedge notched. Five pairs of pseudotracheae. Pleotelson hourglass-shaped. Exopod of uropod tiny.

TYPE SPECIES. *Armadillo clausus* Budde-Lund, 1885. Type by monotypy.

OTHER SPECIES. At least 68 species of *Venezillo* have been described from the New World. Most are poorly characterized.

REMARKS. VAN NAME (1936:335) arranged species of what now are *Cubaris* and *Venezillo* in subgroups according to the morphology of the underedge of pereon I and the absence or size of tubercles on the dorsum.

Venezillo bolivianus (Dollfus, 1897)

Fig. 12F-I

Armadillo bolivianus Dollfus, 1897:1, Fig. 1.

Cubaris boliviana (Dollfus, 1897). VAN NAME, 1936:335, Fig. 200.

Venezillo bolivianus (Dollfus, 1897). ARCANGELI, 1956:14.

DIAGNOSIS. Eyed. Dorsum smooth. Underedge of pereon I with relatively deep notch running its length. Underedges of pereons II and III each with deep notch.

DESCRIPTION. About 13 ocelli. Body with smooth dorsum about 2.9 times as long as broad. Color redish brown. Epistome of cephalon turned up as a more or less sharp, transverse ridge. Two flagellar articles subequal in length. Underedge of pereon I with groove along entire length. Pleotelson hourglass shaped with posterior edge only slightly wider than medial width. Basis with square posterior margin with tiny exopod arising from corner of hourglass shaped pleotelson.

Measurements. 8 mm long (DOLLFUS). 6 mm male described here.

TYPE LOCALITY. "Mission de S. Francisco, Haut Pilcomayo (Bolivie)", Bolivia (first named locality).

DISTRIBUTION. In addition to the type locality in Bolivia, the species was collected at two stations according to Dollfus - Mission de Agauairenda, Chaco Bolivia and Caiza, Chaco Bolivia. In Paraguay one nongravid female 6 mm long was collected at Amambay prov., 80 km S Bella Vista near Ao. Negla, sifting bamboo litter, 11.X.1979. It was collected not far from the new species of *Venezillo* described below.

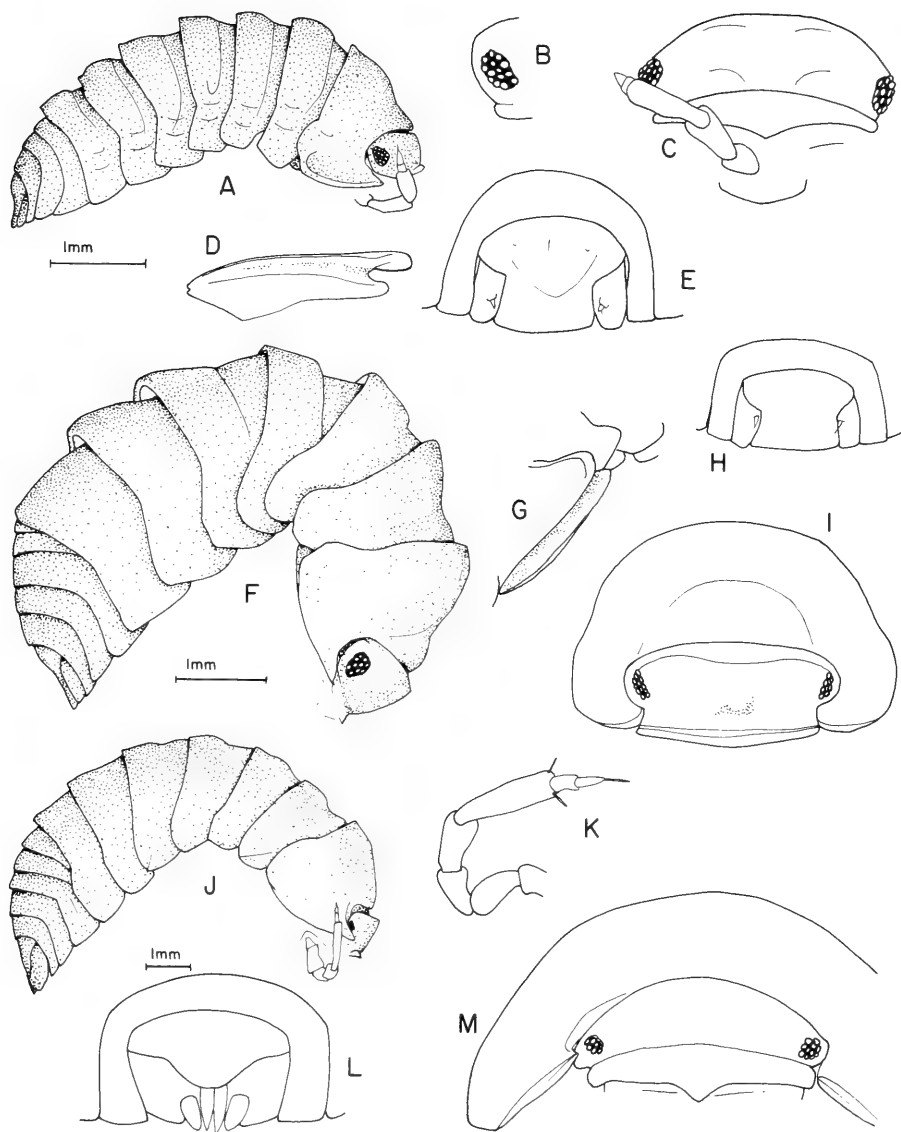


FIG. 12

Venezillo bellavistanus n. sp., female: A) lateral view; B) detail, ocelli; C) cephalon, frontal view; D) detail, underedge pereon I; E) pleotelson, posterior view; F) *Venezillo bolivianus* (Dollfus, 1897), male: G) detail, underedge pereon I; H) pleotelson, posterior view; I) frontal view; J) *Circoniscus bezzii* Arcangeli, 1931, female: K) detail, antenna 2; L) pleotelson, posterior view; M) frontal view.

Deposition of types unknown. Others: MHNG.

TAXONOMIC REMARKS. See "Taxonomic remarks" section for the new species description below.

REMARKS. VAN NAME (1936:335) repeated the description of Dollfus when he recorded the species as *Cubaris boliviana*. Because only one specimen was collected here, it was not dissected and described in detail.

***Venezillo bellavistanus* n. sp.**

Fig. 12A-E

DIAGNOSIS. Eyed. Dorsum with very low tubercles. Underedge of pereon I flattened with large square notch on posterior end, extending anteriorly as very shallow groove. Pereon II notched and III plain.

DESCRIPTION. About 14 ocelli. Dorsum with very low tubercles, about 2.3 times as long as broad. Color gray, marbled. Lateral margins of pereon I slightly flared with notch on posterior part of underedge and extending anteriorly as shallow groove. Underedge of pereon II notched, III plain. Pleotelson hourglass shaped with length of posterior margin only slightly longer than medial width. Basis with rounded posterior corners with tiny exopod arising angularly just below medial length of basis. Exopod of pleopod 1 of female, tiny.

Measurements. Female 4.6 mm long.

TYPE LOCALITY. The species was collected at Amambay prov., 12 km S Bella Vista, sifting forest litter, 23.X.1979: 1 female.

DISTRIBUTION. Known only from the type locality.

Deposition of type: MHNG.

TAXONOMIC REMARKS. The dorsum of the new species and *Venezillo bolivianus* is nearly smooth. *Venezillo bellavistanus* has a short notch on the underedge of pereon I when compared to the long groove on pereon I in *V. bolivianus*. The new species cannot be compared in more detail to other species of *Venezillo* until more specimens including males are collected.

REMARKS. No other species of *Venezillo* has the short notch on pereon I as illustrated.

ACKNOWLEDGEMENT

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Phylogeny of Scaphidiinae with redefinition of tribal and generic limits (Coleoptera: Staphylinidae)

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Phylogeny of Scaphidiinae with redefinition of tribal and generic limits (Coleoptera: Staphylinidae). - The phylogenetic relationships among the higher categories of the Scaphidiinae and genera of the Cypariini, Scaphiini and Scaphidiini are investigated using cladistic analysis. Terminal taxa examined include all genera of these higher taxa except for the Scaphisomatini (including the Heteroscaphini and Toxidiini) for which we examine exemplars. A total of 69 characters (including 3 multistate characters) are enumerated for cladistic analysis. Members of the Apateticinae, Piestinae, and Trigonurinae are used to polarize characters. Two cladograms are produced from the analyses: Cypariina (Scaphiina (Scaphisomatini + Scaphidiina)) and ((Cypariina + Scaphidiina) (Scaphisomatini + Scaphidiina)). On the basis of these cladograms we elevate the subtribes Scaphidiina and Scaphiina to tribal level and eliminate the subtribes Diateliina and Cerambyciscaphina. The following generic level synonymies are made: *Episcaphium* (= *Phenoscapium*), *Scaphidium* (= *Ascaphidium*, *Cribroscaphium*, *Hemiscaphium*, *Falsoascaphidium*, *Scaphidiolum*, *Scaphidopsis*). We review the genera of the Cypariini, Scaphiini and Scaphidiini and provide a catalogue for the described species that includes new combinations resulting from proposed generic synonymies. A replacement name, *Scaphidium pauliani*, is proposed for *Scaphidium sulcatum* Paulian. Information on biology, distribution, and larval descriptions is reviewed for each genus.

Key-words: Coleoptera - Staphylinidae - Scaphidiinae - taxonomy - phylogeny - mycophagy.

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INTRODUCTION

The staphylinid subfamily Scaphidiinae is a taxonomically diverse group of beetles with about 1300 species worldwide (LÖBL, 1992). Most scaphidiine species occur in tropical and subtropical regions with the highest number of described species in southeast Asia; however, the scaphidiine fauna is virtually undescribed in most other tropical regions. The large number of specimens available in museum collections collected by flight-intercept traps, leaf-litter sifting, and canopy fogging indicates that many undescribed species are being discovered regularly.

Scaphidiines are among the most speciose groups of beetles that are strictly mycophagous. Adults may occur on a variety of fungal taxa while oviposition and larval development may be more specialized (NEWTON, 1984). For example, among specialists, some species of *Baeocera* and *Scaphobaocera* (Scaphisomatini) feed exclusively on the spores of myxomycetes (LAWRENCE & NEWTON, 1980; NEWTON, 1984; NEWTON & STEPHENSON, 1990; NEWTON, 1991), and species of *Scaphium* and *Cyparium* usually feed on the fruiting bodies of Agaricales and other fleshy Basidiomycetes (ASHE, 1982; NEWTON, 1984; KOMPANTSEV & POTOTSKAYA, 1987). Because of their fungal host patterns, scaphidiines are an attractive group to be studied for patterns of mycophagy from both ecological and phylogenetic perspectives.

Most of the species of Scaphidiinae are small (1.0-3.0 mm) and black or reddish-brown in colour; however, some groups of genera have species that may be larger (11 mm or more) with striking colour patterns. Many species of scaphidiines exhibit male secondary sexual characteristics besides dilated protarsomeres (and sometimes the mesotarsomeres) that occur in many groups of staphylinoids. For example, both sexes of *Diatelium wallacei* (Fig. 1) have extremely long necks; however, only some male specimens have necks that attain lengths greater than the lengths of their bodies. All male specimens of the subtribe Scaphidiina have well-developed setiferous patches on their metasterna. The setae are curled at their ends and at the base of each seta there are 2-3 small pores (Figs 18,19); usually setae occurring on other parts of the body have only a single associated pore. The setiferous patches appear to be similar to sex patches of male beetles described by FAUSTINI & HALSTEAD (1982). Males of *Scaphidium* and *Euscapidium* have stridulatory files on the prescutum that articulate with corresponding plectra on the inner posterior margin of the pronotum (Figs 17, 32). The numbers of files vary from 7 to 11. Curiously, the pronota of males in some of these species have a large median hump that may be related to the function of the scutellary file.

The first scaphidiine species was described in 1758 by Linné and suprageneric rank was given to the group by LATREILLE (1807). Since LECONTE & HORN (1883), the scaphidiines were treated as a family and usually placed close to the staphylinids. CASEY (1893) distinguished two groups among the Scaphidiidae: the Scaphidiini and the Scaphisomatini (incorrectly spelled as Scaphisomini). Subsequently, ACHARD (1914) and PIC (1915b) erected the tribes Cerambyciscaphini and Heteroscaphini, respectively. ACHARD (1924) proposed a new classification for the 41 genera that he recognized. Many characters on which his tribes and subtribes were based are variable

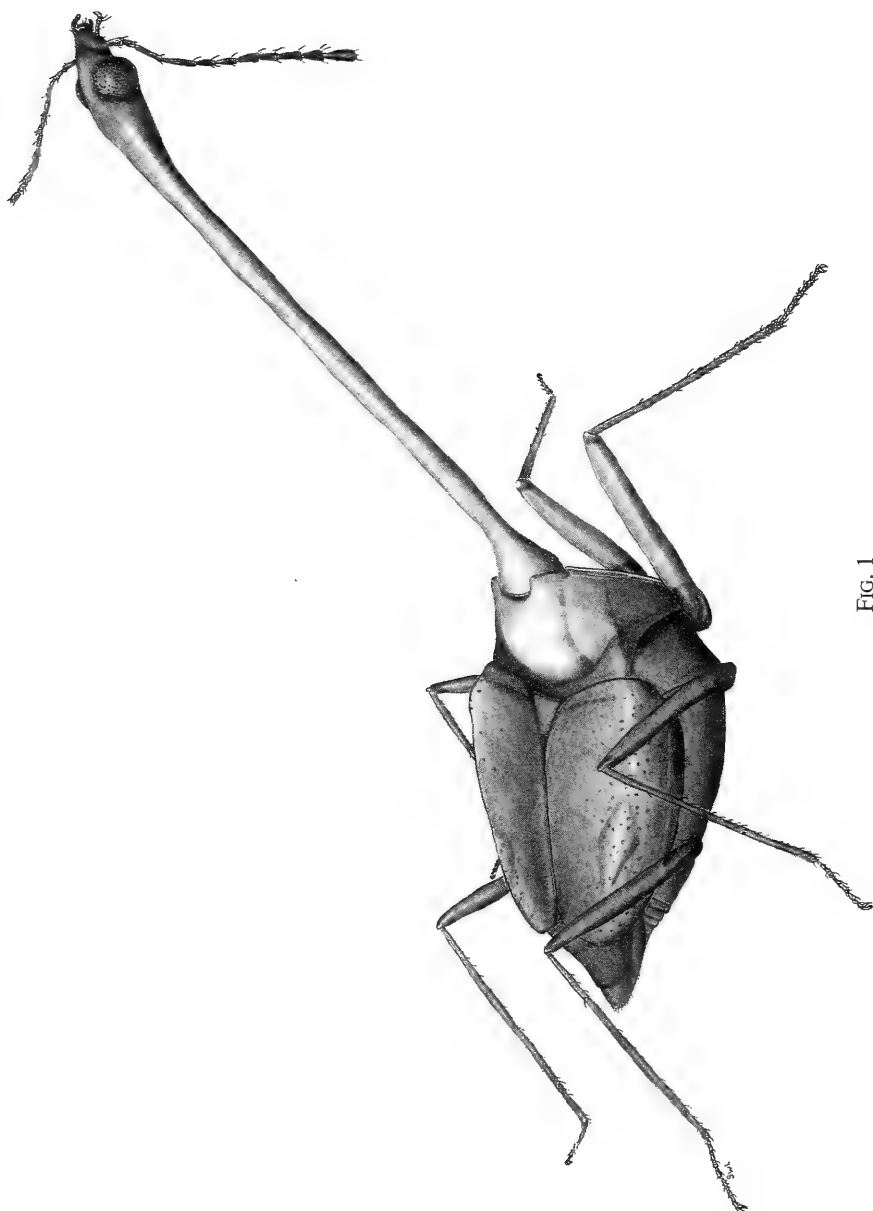


FIG. 1
Habitus of *Diatelim wallacei*, lateral view.

and inconsistent among the higher categories. Achard's classification was essentially ignored by subsequent workers. KASULE (1966), in a study of the larvae of British Staphylinidae, recognized that scaphidiid larvae share many characteristics with some members of the Staphylinidae and changed the status of the family to subfamily, placing the group near the Euaesthetinae and Oxyporinae. Perhaps ignorant of Kasule's work, TAMANINI (1969) separated the Scaphidiidae into two families, the Scaphidiidae and Scaphisomidae, based mainly upon characters of the prosternum and antennae. Recognizing natural affinities as Kasule did, LAWRENCE & NEWTON (1982) placed the scaphidiids in their "oxyteline group" of Staphylinidae, and currently LAWRENCE (1991) and NEWTON & THAYER (1992) treat the scaphidiids as a subfamily. The current classification is shown in Table 1.

To date no classification has been proposed for the Scaphidiinae based on a sound phylogenetic analysis, and the classification of the Scaphidiinae has essentially remained unchanged since ACHARD (1924) with modifications of family-group names (NEWTON & THAYER, 1992). In the present study the phylogenetic relationships of the higher categories will be studied, the genera that have been placed in the tribes Scaphidiini and Cypariini are reviewed, and a catalogue for the included species (Appendix) is provided.

MATERIALS AND METHODS

Examinations of characters are made from pinned, glycerin-dissected, and slide-mounted adult specimens. First, beetle specimens are placed in cold KOH (10% solution) until the internal tissues are macerated. Further clearing of the cuticle in hydrogen peroxide is necessary for some specimens. After rinsing in water, specimens are placed into glycerin (for glycerin-dissections) or into serial solutions of water:alcohol (until water is removed) for slide-mount preparations. The cleared beetle is placed into a drop of Euparal (Chroma-Gesellschaft, Kongen/Necker) on a microslide and the dissection performed using fine dissecting needles. Once the beetle is dissarticulated and the parts properly arranged, the dissection is dried for two hours until the dissected parts are stationary. To prevent crushing of larger specimens, cover-slip props are inserted into the Euparal. The dissection is placed on a slide drier for 24 hours, then additional layers of Euparal are added to the specimen and the cover-slip applied. Thorough drying requires about two weeks. Pinned specimens are examined for external characters. Internal characters in rare taxa are examined in specimens that are softened in water. Dissection of genitalia from pinned specimens follows that of LESCHEN & *al.* (1989). Specimens examined are deposited in the Muséum d'histoire naturelle, Geneva, Muséum National d'Histoire Naturelle, Paris, Museo Civico di Storia Naturale, Genova, Snow Entomological Museum, University of Kansas, Lawrence, and the R. Leschen collection.

Terminology for some external structures we use is described in LESCHEN & *al.* (1989). Lengths of beetles are measured from the apex of the head to the tip of the elytra.

Terminal taxa for the phylogenetic analysis include all genera of the Cyperiini and Scaphidiini. Several generic level synonymies that we establish within the Scaphidiinae are based on unique and unreversed synapomorphies (see taxonomic sections for details). Also, ACHARD (1924) recognized the Heteroscaphini and Toxidiini as separate tribes from the remaining Scaphidiinae. On the basis of unique and unreversed characters (procoxal cavity, see character 25; mesosternal process anvil-shaped, filiform antennomeres) we believe that the Scaphisomatini, Heteroscaphini, and Toxidiini, should be grouped together and that the two latter taxa should be included as subtribes in the Scaphisomatini. Monophyly of each of the subtribes in the Scaphisomatini is questionable. Species examined among the Cyperiini, Scaphidiina, and Scaphiina are indicated in the species catalogue (Appendix). Members of the following Scaphisomatini are examined: *Baeoceridium* Reitter, *Vituratella* Reitter, *Scaphisoma* Leach, *Baeocera* Erichson, *Scaphobaeocera* Csiki, *Toxidium* LeConte, *Bironium* Csiki, *Pseudobironium* Pic, and *Birocera* Löbl.

Determinations of character state polarities are based on outgroup comparisons to the subfamilies Apateticinae (*Apatetica princeps* Sharp and *Nodynus leucofasciatus* Lewis), Piestinae (*Siagonium* spp. and *Ziophorus* spp.), and Trigonurinae (*Trigonurus asiaticus* Reiche) which together with the Scaphidiinae are members of the oxyteline group of staphylinids (LAWRENCE & NEWTON, 1982). Scaphidiines most closely resemble members of the Apateticinae based on the form of the elytra that cover abdominal tergites 1 and 2 and the form of the abdomen that is abruptly narrowed posteriorly and not parallel-sided (like most members of the Oxyteline group). Until there is a phylogenetic hypothesis of the higher taxa of the oxyteline group, the definitive sister relationship of the Scaphidiinae is unknown.

Characters enumerated for phylogenetic analysis from adult specimens are hypothesized to be homologous. Details regarding determination and evaluation of characters, their states, and polarities are discussed in the section on character analysis. Data are binary coded and entered into MacClade version 3 (MADDISON & MADDISON, 1992). Numbers for characters correspond to those in the data matrix, character analysis, and cladograms. Characters are mapped onto cladograms using ACCTRAN optimization (MADDISON & *al.*, 1984).

Because the relationships among the outgroup taxa, and the remaining members of the oxyteline group are unknown, we perform separate analyses using different specifications for outgroup taxa. One analysis is based upon the inclusion of all three members of the outgroups, Piestinae, Trigonurinae, and Apateticinae, as terminal outgroup taxa (we specify that these form a monophyletic group). In the other analysis a generalized outgroup is constructed from the three taxa; and, any polymorphism among the outgroup is coded in the data matrix entered into MacClade. When different outgroup taxa are used in the phylogenetic analysis, polarities of characters should change resulting in different tree topologies.

Phylogenetic analyses are performed with PAUP 3.1.1 (Swofford, 1993) and character analysis assisted with MacClade. All multistate characters are treated as unordered and all characters are assigned equal weight in PAUP. We used the heuristic

tree search option for generating cladograms with the following options: branch swapping on all starting trees (even non-minimal trees), branch swapping with steepest descent, and the addition sequence random. Alternative branching patterns were examined with MacClade.

At the beginning of this study it was not clear to us that *Kathetopodion borneense* (Pic) was a member of the Scaphisomatini. Two features of this species are similar to those of the outgroups; the tarsomeres are relatively thick (not thin and elongate as they are in members of the Scaphisomatini) and the head is somewhat prognathous. We decided to include *K. borneense* as a terminal taxon and allow the parsimony analysis to determine the placement of the species.

CHARACTER ANALYSIS

Characters used for reconstructing the phylogeny of the Scaphidiinae are listed below and each description indicates how polarities have been interpreted for each character. The number of each character corresponds to the characters as they appear in the data matrix (Table 3) and the cladogram (Fig. 40). The number in parentheses indicates how each state is coded in transformation series for each character. Plesiomorphies appear first followed by apomorphies.

For many of the characters it is necessary to have adequate dissections for observation. Because there is a lack of specimens for some scaphidiines, species could not be dissected entirely; and these include the following: *Euscaphidium tuberosum* Achard (2 males), *Cerambyciscapha dohertyi* Pic (1 male), and *Kathetopodion borneense* (Pic) (2 females).

1. HYPOPHARYNGEAL SETAE (Figs 20, 21, 30). (0) Arranged into a peripheral comb of evenly spaced setae surrounding the hypopharynx; (1) without peripheral comb of setae. All members of the ingroup have scattered setae on the hypopharynx but lack the distinct setal comb present in most species of Staphylinidae. The distribution of the setae among the ingroup taxa varies. The setae are scattered on the entire surface of the hypopharynx (*Scaphium*) or confined to lateral portions (other taxa examined). The hypopharyngeal setae may be elongate (*Scaphium*) or short (Scaphisomatini) or composed of different sizes (in some members of the Scaphidiina). The variation of the hypopharyngeal setae appears to be species specific and may not be appropriate for higher level analyses. Character state (1) does not occur in the outgroup and it is therefore inferred to be apomorphic.

2. GALEAL SETAE (Figs 26, 27). (0) Elongate and not bristle-like; (1) short and bristle-like. All members of the ingroup have setae that are shortened, and arranged into distinct rows. Among the outgroup taxa, the setae are elongate and either arranged into rows (members of the Piestinae and Trigonurinae) or not (members of the Apatecinae). The setae on the galea of members of the Scaphidiinae are bent, or slightly bent, and spatulate at their apices. Character state (1) does not occur in the outgroup and it is, therefore, inferred as apomorphic.

3. SHAPE OF THE LACINIA (Figs 26, 27). (0) Broadly flattened with a well-developed hyaline inner margin; (1) not especially flattened with a poorly developed hyaline inner margin. Among members of the outgroup the lacinia is a broad appendage that has a large hyaline margin that bears setae along its inner edge. In contrast, most members of the Scaphidiinae have a comparatively narrower lacinia with a reduced hyaline region that bares elongate setae at its apical and subapical margins. In *Kathetopodion* the lacinia is flattened and hyaline and is similar to that observed in the outgroup. Character state (1) is absent from the outgroup and it is, therefore, inferred to be apomorphic.

4. APEX OF THE MANDIBLE (Figs 22, 24). (0) With one incisor lobe; (1) with two teeth. Among members of the Scaphidiini and *Cyparium*, and some members of the Scaphisomatini, the mandible has two apical teeth and in other members of the Scaphisomatini there are taxa that have a simple or bifid apex. In the latter taxon this character is coded as polymorphic. Among members of the outgroup, the Piestinae have two or three teeth, and these are located at the margins of the mandible. It is not clear as to whether or not the lateral teeth in Piestinae are homologous to the subapical teeth in Scaphidiinae. The mandibles of Piestinae are not as dorsoventrally flattened and their lateral teeth are more strongly produced than those of Scaphidiinae. Although unlikely, it is possible that scaphidiine subapical teeth are derived from lateral teeth present in an ancestor and they have subsequently moved to a distal position. Until outgroup relationships are resolved and variation among oxyteline group members is investigated, the polarity of this character is equivocal.

5. SUBAPICAL SERRATIONS ON THE INCISING MARGIN OF THE RIGHT MANDIBLE. (0) Absent; (1) present. Except for *Kathetopodion*, all specimens examined of the ingroup have a serrate margin on the subapical edge of the mandible. Members of the outgroup do not have the serrate margin and, therefore, character state (1) is inferred as apomorphic.

6. SETAE ON THE ANTERIOR MARGIN OF THE LABRUM (Figs 23, 25). (0) Frayed; (1) bifid. Among members of the oxyteline group, the setae along the margin of the labrum may be simple or modified in forms that are apically frayed, branched, or barbed along the shafts. Among the ingroup, *Kathetopodion* and the Scaphidiina have labral setae that are relatively short and apically bifid, the setae are somewhat frayed in the Scaphiina, and among members of the Scaphisomatini there are short setae that are either simple or apically bifid (this character is coded as polymorphic for the Scaphisomatini). Character state (1), present among the ingroup, is inferred as apomorphic.

7. SHAPE OF LABRUM (Figs 23, 25). (0) Deeply emarginate; (1) not deeply emarginate. Among members of the outgroup, the labrum is deeply incised and somewhat v-shaped. In contrast, among members of the ingroup the labrum is slightly emarginate. Character state (1) is absent in the outgroup, and it is, therefore, inferred as apomorphic.

8. EPIPHARYNX (Figs 23, 25). (0) With peg-like sensilla; (1) without peg-like sensilla. All members of the ingroup, with the exception of *Cerambyciscapha*, and the Piestinae have campaniform sensilla present at the surface of the epipharynx. Members of *Trigonurus*, Apateticinae, and *Cerambyciscapha* have peg-like sensilla at the surface of the epipharynx. Until phylogenetic relationships among the outgroup are known, polarity of this character is uncertain.

9. SHAPE OF ANTENNAL CLUB IN CROSS-SECTIONAL VIEW (Fig. 14). (0) Round; (1) slightly flattened, (2) completely flattened. Among members of the outgroup, the antennomeres are rounded in cross-section, and are typically 2 times longer than wide. Among the ingroup taxa there are two additional states associated with the form of the antennal club; the antennomeres are slightly flattened and compressed (1) or the antennomeres are completely flattened (2). Among scaphisomatines, some taxa (such as *Bironium*) have elongate antennomeres (many times longer than wide) that are filiform and rounded in cross section. This character is coded as polymorphic for the Scaphisomatini. Character states (1) and (2) do not occur in the outgroups, and, therefore, these are inferred as apomorphic.

10. ANTENNOMERES 3 - 11. (0) Symmetrical; (1) asymmetrical. All members of the outgroup have antennomeres that are symmetrical. Among the ingroup taxa, only some members of the Scaphisomatini and *Kathetopodion* have antennomeres that are asymmetrical in shape. In other scaphisomatines, such as *Bironium*, the antennomeres are not flattened or asymmetrical, and this character is coded as polymorphic for this tribe. Character state (1) does not occur in the outgroup and it is, therefore, inferred as apomorphic.

11. ANTENNOMERE 8. (0) Equal in size to antennomeres 7 and 9; (1) reduced, smaller than antennomeres 7 and 9. Antennomere 8 is equal in size and proportion to other antennomeres forming the club among members of the outgroup, the Scaphidiini and *Cyparium*. Antennomere 8 is reduced in *Kathetopodion* and most members of the Scaphisomatini (antennomere 8 is equal in length to 7 and 9 in specimens of *Bironium*). This character is coded as polymorphic for the Scaphisomatini. Character state (1) does not occur in the outgroup and it is, therefore, considered to be apomorphic.

12. ANTENNAL INSERTION. (0) Hidden below the frons; (1) visible. Among members of the outgroup, the frons is well-developed, concealing the antennal insertions in dorsal view. In all members of the scaphidiines the frons is highly reduced such that the antennal insertions are visible in dorsal view. Character state (1) is absent in the outgroup and it is, therefore, inferred as apomorphic.

13. EYE. (0) Entire; (1) notched. Among members of the outgroup, the eye is entire (0). In the scaphidiines, the eye may be notched at the antennal insertion. This condition is variable in members of the Scaphisomatini. The eye is entire in members of *Scaphium*, *Cyparium*, *Kathetopodion*, and some members of the Scaphisomatini. The character is coded as polymorphic for the Scaphisomatini. Character state (1) is absent in the outgroup and it is, therefore, considered as apomorphic.

14. TEMPORAL REGION OF THE HEAD (Figs 1, 2, 3). (0) Extending posteriorly a length as long as that of the eye, a neck is present; (1) less than $1/4$ the width of the eye, a neck is absent; (2) at least 3 times the length of the eye. A distinct temporal region that is constricted behind the eyes and inserts into the prothorax is present among all members of the outgroup. This condition is also present in members of the Scaphiina; but, a distinct temporal region is absent among the remaining members of the scaphidiines. Unique among staphylinoids, the unusually long neck of the species *Diatelium wallacei* Pascoe (character state (2)) is typically longer than the prothorax. Character states (1) and (2) are found among members of the ingroup and character state (0), present in the outgroup, suggests character states (1) and (2) are apomorphic.

15. GULAR SUTURES (Figs 2, 3). (0) Separate; (1) fused. The gular sutures at the base of the head are separated and form a distinct gula in members of the Trigonurinae, Apateticinae, and *Siagonium* (Fig. 2). The gular sutures are fused in all members of the scaphidiines (Fig. 3). A specimen of *Zirophorus* appears to have contiguous gular sutures, although the endocarinae (which form part of the tentorium) remain separate. The Piestinae are coded as polymorphic for this character. The form of the gula is variable in staphylinids (EVANS, 1965), and the distribution of character states among the oxyteline groups is unknown. Polarity of this character is uncertain because of the variable distribution of character states in the outgroup.

16. ENDOCARINA AT BASE OF THE HEAD. (0) Present along entire length of the gular region of the head; (1) present along half of the length of the gular region of the head. Fusion of the gular sutures is associated with the development of a single endocarina at the floor of the head that forms part of the tentorium. Among members of the outgroup taxa that have a distinct gula, the endocarina is present along the floor of the head. Among members of the Scaphiina and some members of the Scaphisomatini this endocarina is present only in the basal half of the head. The character is coded as polymorphic in the Scaphisomatini. The endocarina is not visible (possibly absent) in the dissected specimen of *Diatelium* and we coded this character as (?) for this species. Character state (1) is not present in the outgroup and it is, therefore, inferred as apomorphic. This character is not observed in specimens of *Euscapidium* and *Cerambyciscapha*.

17. SHAPE OF THE MENTUM. (0) Wider than long and rectangular; (1) about as long as wide and trapezoidal. The mentum occurs as a broad rectangular plate among members of the outgroup taxa. The mentum is reduced in size among members of the Scaphidiinae, and its length and width vary among members of the Scaphisomatini. The character state is coded as a polymorphism for the Scaphisomatini. Character state (1) is absent in the outgroup and it is, therefore, inferred as apomorphic. This character is not observed in the specimen of *Cerambyciscapha*.

18. POSTERIOR ANGLE OF THE PRONOTUM. (0) Rounded; (1) pointed. The posterior pronotal angle is rounded among members of the outgroup taxa. The shape of the posterior pronotal angle among ingroup taxa varies from rounded (among members of the

Scaphiina) to pointed (in members of the Scaphidiina). Both character states occur in members of *Episcaphium* and the Scaphisomatini: the character is coded as polymorphic in these taxa.

The general shape of the pronotum differs in the Scaphidiinae compared to the remaining members of the oxyteline group and other staphylinids. The pronotum in the scaphidiines is box-shaped with a large pronotal volume (HLAVAC 1975). Due to the form of the prothorax, the posterior angle, composed of the terminal juncture of the hypopleuron and the pronotum, meet at a more or less 90° angle. In contrast, the hypopleuron and the pronotum among other staphylinids either meet at a relatively low angle (Apateticinae) or, as in the case of Piestinae, a distinct posterior angle is absent and the pronotal margin has a complete bead that rests on the hypopleuron. The variation among prothorax types among outgroups cause difficulties in defining character states. When only the variation in the Scaphidiinae is considered: an angle that is pointed (character state 1) is defined by the presence of a posterior angle that is produced beyond the hind margin of the pronotum and there is a distinct angular termination. Because this condition is absent among members of the outgroup, character state (1) is inferred as apomorphic.

19. POSTERIOR ANGLE OF THE PROTHORAX MOLDED ONTO THE ANTERIOR ANGLE OF THE ELYTRON. (0) Absent; (1) present. The pronotal angle may be molded into a recess located at the anterior angle of the elytron. Members of *Episcaphium* and the Scaphisomatini are coded as polymorphic for this character. Character state (1), absent in members of the outgroup, is therefore considered as apomorphic.

20. BASAL TRANSVERSE STRIA ON THE PRONOTUM. (0) Absent; (1) present. A punctate stria at the basal portion of the pronotum is present in members of the Scaphidiini (absent in some species of *Scaphidium*), *Ascaphidium*, and *Episcaphium*. This stria is absent among the remaining members of the Scaphidiinae and the outgroup taxa. This character is coded as polymorphic for *Scaphidium*. Character state (1) is absent in the outgroup and it is, therefore, inferred as apomorphic.

21. PRONOTUM WITH MARGINAL BEAD. (0) Absent; (1) present. A distinct marginal bead on the pronotum is absent in members of *Trigonurus* and *Apatetica*. This character is coded as a polymorphism for Apateticinae. Determination of the polarity of these character states is uncertain because the phylogenetic relationships among members of the outgroup are unknown.

22. HYPOMERON. (0) Small; (1) large. Stated previously (see character 18) the pronotum of scaphidiines is unusual among the oxyteline group. An unusually large hypomeron, present in the Scaphidiinae, is one of several features associated with the modified prothorax (i.e., prothorax narrowed apically, high pronotal volume, posterior margin undulate, general reduction in the size of the prosternum (see character 23)). We code only the hypomeron as representative of the entire complex of characters. The presence of a relatively small hypomeron (0), present in the outgroup, suggests that a relatively large hypomeron (1), present in members of the Scaphidiinae, is apomorphic.

23. PROSTERNUM IN FRONT OF PROCOXAE (Figs 4-6, 15, 31). (0) Well-developed, at least a length equal to 3/4 procoxal width; (1) reduced to a length less than that of coxae. Because the length of the prosternum in front of the procoxa is very variable among members of the scaphidiines and among the outgroup partitioning this character into several discrete character states is difficult. Polarity of this character is also difficult without a phylogenetic hypothesis for the outgroup. Therefore, character coding is simplified to represent the extremes in the variation observed. Only the Scaphisomatini (Fig. 6) and *Cyparium* have a highly reduced prosternum in contrast to the remaining members of the Scaphidiinae and the outgroups that have a relatively larger prosternum. The presence of a large and distinct prosternum among members of the outgroup taxa suggests that character state (1) is apomorphic.

24. PROCOXAL CAVITY (Figs 4-6, 15, 31). (0) Partially closed behind; (1) completely open behind. The procoxal cavities among members of the outgroup taxa are partially closed behind by posterior flanges of the prosternum such that the procoxae do not contact the mesosternum. Among members of the Scaphidiinae, the procoxal cavities are not enclosed by the posterior flanges of the prosternum, and contact the mesosternum. Character state (1) is absent in the outgroup and is it therefore inferred as apomorphic.

25. PROCOXAL CAVITY (Figs 4-6, 15, 31) (0) Internally open; (1) internally closed by the prosternum; (2) internally closed by the fusion of the prosternum and hypomeron. The procoxae of scaphidiines are subtended by the prosternum, forming a broad internal bar or shelf supporting the coxae (1). In Scaphisomatini the prosternum is fused with the hypomeron thereby forming complete internal closure of the procoxal cavity (2). Among members of the outgroup the procoxal cavity is completely open internally and, therefore, characters states (1) and (2) are inferred as apomorphic.

26. KEEL ON MESOSTERNUM (Figs 12, 13, 16). (0) Absent; (1) present. A well-developed keel on the midline of the mesosternum that inserts into the median space of the procoxae, is present among all members of the Scaphidiinae. Character state (1), absent among members of the outgroup, is inferred as apomorphic.

27. TRANSVERSE MESOSTERNAL RIDGE. (0) Absent; (1) present. A transverse ridge on the mesosternum, directly behind the keel, occurs in members of *Scaphium*, *Episcaphium*, and some species of *Scaphidium*. This character is coded as polymorphic for *Scaphidium*. Character state (1) is completely absent in the outgroup and it is, therefore, inferred as apomorphic.

28. ANVIL-LIKE PROCESS OF THE MESOSTERNUM. (0) Absent; (1) present. The members of the Scaphisomatini, including *Kathetopodion*, possess an anvil-like process on the mesosternal keel, which is absent in the remaining members of the Scaphidiinae and the outgroup. The process is variable: it may be diamond-shaped or triangulate in ventral view and is flattened on its ventral face where a small keel may be present. Character state (1) is absent in the outgroup and it is, therefore, inferred as apomorphic.

29. WIDTH OF MESOSTERNAL PROCESS (Figs 12, 13, 16). (0) Less than the width of mesocoxa; (1) equal to the width of mesocoxa; (2) more than width of mesocoxa. Among the outgroup taxa, the mesocoxae are approximate, separated by a relatively narrow mesosternal process. The width of the mesosternal process is equal to that of the mesocoxa in members of *Ascaphium*, some *Episcaphium*, *Scaphium*, *Kathetopodion* and other Scaphisomatini. The width of the mesosternal process exceeds that of the mesocoxa in the Scaphidiina, some members of the Scaphisomatini, and some members of *Episcaphium*. In the latter two groups, widths of the mesosternum are variable and the character is coded as a polymorphic for these taxa. Because the outgroup taxa have a narrow mesosternal process, character states (1) and (2) are inferred as apomorphic.

30. PROCESS AT ANTERIOR REGION OF MESOTHORAX. (0) Present; (1) absent. On the anterior portion of the mesothorax of members of the Scaphidiina there is a process that inserts into the lateral portion of the inner wall of the prothorax. This process is absent among the remaining members of the Scaphidiinae. The absence of character state (1) in the outgroup suggests that it is apomorphic.

31. SUBMESOCOXYAL LINES AT MIDDLE OF METASTERNUM (Figs 12, 13, 16). (0) Not connected; (1) connected. Among members of the Apateticinae and Scaphidiinae there are submesocoxal lines that parallel the mesocoxal cavities that may end near the inner portion of the metasternum. These lines are connected at the middle of the metasternum among members of the Scaphiina (or not as in some *Episcaphium*), *Cyparium*, and some Scaphisomatini: this character is coded as polymorphic for the Scaphisomatini and *Episcaphium*. Although members of the Piestinae and Trigonurinae do not possess these lines, the presence of these in the scaphidiines and apateticines suggests that the lines may have been part of the groundplan of the Scaphidiinae. However, there is no phylogenetic information available for the outgroups, the Apateticines may not be sister taxa to the Scaphidiinae, and, therefore, polarity of this character is uncertain.

32. SUBMESOCOXYAL LINES (Figs 12, 13, 16). (0) Without punctures; (1) with punctures. The submesocoxal lines bear punctures in most members of the Scaphidiinae, but punctures are absent in some members of the Scaphisomatini and in members of the Apateticinae. This character is coded as polymorphic for the Scaphisomatini. We infer that character state (1) is apomorphic because it is absent among members of the Apateticinae and submesocoxal lines are completely absent among the other members of the outgroup.

33. LONGITUDINAL LINE IN THE MIDLINE OF THE METASTERNUM (Figs 12, 18). (0) Absent; (1) present. This structure is observed in specimens that are either light in color or those that have been cleared for dissection. The longitudinal line is present only in members of the Scaphidiina. The absence of character state (1) in the outgroup suggests that it is apomorphic. This character is not observed in specimens of *Euscaphidium* and *Kathetopodion*.

34. PREMETACOXAL LINES ON METASTERNUM. (0) Present; (1) absent. Premetacoxal lines are present in most members of the Scaphidiinae, but are absent in a few members of the Scaphisomatini. These lines are absent in specimens of *Trigonurus* and *Nodynus*. This character is coded as polymorphic for the Apateticinae and Scaphisomatini. The lines, present on the external portion of the metasternum, are associated with transverse endocarinae that articulate with the anterior portions of the metacoxae. Because of character variation and lack of phylogenetic resolution among the outgroup, determination of the polarity of this character is uncertain.

35. METASTERNAL PROCESS (Figs 13, 16). (0) Absent; (1) present. Among members of the Scaphiina, *Cyparium*, some Scaphisomatini, and some species of *Scaphidium* there is a distinct metasternal process separating the metacoxae. This process is often delimited anteriorly by a visible thin line, or when cleared, is delimited by an endocarina visible through the cuticle where its edge is part of an endocarina that serves as part of an attachment site for the metendosternite. Sometimes the metasternal process bears smaller terminal processes (often present in males of some species) and it may be divided by a thin line along its midline. This character is coded as polymorphic for the Scaphisomatini and *Scaphidium*. Members of the outgroup lack character state (1) and it is, therefore, inferred as apomorphic.

36. METASTERNUM WITH ONLY ONE MACROSETA PER SIDE (Figs 13, 16). (0) Absent, or with more than 1 seta per side; (1) present. The metasternum bears one seta per side among members of *Cyparium*, Scaphiina, and Scaphisomatini. In one specimen of *Episcaphium* there are two setae on one side of the metasternum. This character is variable in *Episcaphium* and Scaphisomatini and these are coded as polymorphic for this character. Among members of the outgroup, the Apateticinae and *Trigonurus* completely lack the macrosetae, in contrast there are 2 macrosetae per side in *Siagonium* and 4 per side in *Zirophorus*. Determining the groundplan for this character is problematic because the numbers of macrosetae vary in the outgroup and there is a lack of phylogenetic information for the outgroup relationships.

37. METASTERNUM OF MALE WITH SETIFEROUS SEX PATCH (Figs 13, 16, 18, 19). (0) Absent; (1) present. The metasternum of male specimens of the Scaphidiina possess a patch of closely packed setae that are curled at their ends. Males of some members of Scaphisomatini (such as some species of *Baeocera*) have macrosetae, but differ from those in the Scaphidiina in that these are not closely packed and do not have curled ends. The different appearance of the setiferous male patches among the Scaphidiina and Scaphisomatini suggests that this character is homoplastic. Male specimens of members of the outgroup taxa do not have character state (1) and it is, therefore, inferred as apomorphic. Male specimens of *Kathetopodion* are unknown.

38. METACOXAE. (0) Approximate; (1) separate. The metacoxae among the members of the outgroup taxa are approximate, separated by a narrow intercoxal process arising from the first visible abdominal sternite. Among all members of the scaphidiines, with

exception of those taxa that are laterally compressed in the Scaphisomatini (e.g., *Scaphobaeocera* and *Toxidium*), the metacoxae are separate and there is a relatively broad intercoxal process. This character is coded as polymorphic for the Scaphisomatini. Character state (1) is absent in the outgroup taxa and it is, therefore, inferred as apomorphic.

39. ANTERIOR ARMS OF THE METENDOSTERNITE (Figs 10, 33). (0) Present; (1) absent. The anterior arms of the metendosternite among members of the outgroup taxa are well-developed (Fig. 33); in contrast, all members of the scaphidiines completely lack the anterior tendons. In scaphidiines the anterior tendons may have moved into a terminal position where the apices of the furcal arms are somewhat expanded or frayed. Another feature of the metendosternite that appears to be tightly coupled with the reduction of the frontal arms is a shortening of the median stalk. Because both of these characters covary, we do not treat a shortened stalk as a separate character. Reduction of the anterior tendons (1) does not occur in members of the outgroup and are considered as apomorphic. This character is not observed in specimens of *Euscaphidium*, *Cerambyciscapha*, and *Kathetopodion*.

40. MEDIAN CARINA ON THE STALK OF THE METENDOSTERNITE (Figs 10, 33, 34). (0) Absent; (1) present. A median carina is present on the stalk of the metendosternite in members of the Scaphiina, *Cyparium*, and some Scaphisomatini. This character is also present in a dissected specimen of *Zirophorus*. This character state is coded as polymorphic for the Piestinae and Scaphisomatini. Character state polarity for this character is uncertain because of the lack knowledge about the phylogenetic relationships of and variation of the metendosternite among members of the outgroup. This character is not observed in specimens of *Euscaphidium*, *Cerambyciscapha*, and *Kathetopodion*.

41. STRIDULATORY FILE ON THE PRESCUTUM OF THE MALE (Fig. 17). (0) Absent; (1) present. A stridulatory file is present on the prescutum of male specimens among members of the Scaphidiina. Character state (1) is absent among members of the outgroup and it is, therefore, inferred as apomorphic. Male specimens are unknown for *Kathetopodion*.

42. VISIBLE PORTION OF SCUTELLUM. (0) Almost as large as entire mesonotum; (1) 1/2 to 1/4 as large as entire mesonotum. The size of the scutellum is relatively large in relation to that of the entire mesonotum among members of the outgroup; in contrast, it is relatively small among members of the Scaphidiinae. Among some members of the Scaphisomatini, the scutellum may be reduced to a size barely visible at the base of the elytra or completely absent. The absence of character state (1) in the outgroup suggests that it is apomorphic.

43. EPIPLEURON IN LATERAL VIEW. (0) Oblique; (1) almost vertical. The relative angle of the epipleuron in relation to the horizontal plane of the body is oblique among members of the Apateticinae, *Trigonurus*, *Cyparium*, *Kathetopodion*, and some members of the

Scaphisomatini. The epipleuron is relatively vertical in members of the Piestinae, some members of the Scaphisomatini and Scaphidiini. This character is coded as polymorphic for the Scaphisomatini. Polarity of this character is uncertain because of the lack of information regarding phylogenetic relationships and variable distribution of character states among members of the outgroup.

44. POSTERIOR MARGIN OF THE ELYTRON. (0) Without serrations; (1) with serrations. The posterior edge of the elytron in members of the Scaphidiinae typically has a serrate margin composed of widely spaced teeth that are directed laterally, away from the midline. The teeth may line the posterior edge to the inner flange of the elytron: the teeth are more spine-like at the inner flange of the elytron. Most members of the Scaphidiinae have a serrate edge, but it is absent in some species of Scaphisomatini and *Scaphium*; for these taxa this character is coded as polymorphic. Among members of the outgroup, similar structures occur in species of the Piestinae. In contrast to the regularly spaced teeth of the Scaphidiinae, the teeth on the posterior edge of the elytron in the observed Piestinae are irregular and are directed posteriorly, suggesting that the condition in the Piestinae may not be homologous to that found in Scaphidiinae. Polarity of this character is uncertain because of the lack of information regarding phylogenetic relationships of and variable distribution of character states among members of the outgroup.

45. INTERLOCKING TEETH ON THE INNER MARGIN OF THE ELYTRON. (0) Absent; (1) present. Among members of the Scaphidiina and Scaphisomatini there is an elytral interlocking mechanism at the inner sutural margins of the basal part of the elytra. It consists of a series of small teeth that fit into corresponding sockets. Among members of the Scaphidiina the teeth are undulate and smooth-sided, in contrast, those of the Scaphisomatini are jagged and pointed. On the basis of their different microstructure this character may be homoplastic. Character state (1) is absent among members of the outgroup and it is, therefore, inferred as apomorphic. This character is not observed in specimens of *Euscaphidium*, *Cerambyciscapha*, and *Kathetopodion*.

46. ABDOMINAL SPIRACLES 1 to 3. (0) In sclerotized region of the terga; (1) in membranous region of the terga. Like other members of the Staphylinidae, there has been extensive modification of the abdomen, especially in the reduction and fusion of the number of tergal elements. Among members of the Scaphidiinae there is a general reduction in the number of paratergites (see characters 48-52): they are no longer sclerotized and it is difficult to distinguish them from adjacent intersegmental membranes. Among members of the Scaphidiinae, abdominal spiracles 1-3 (or 1-2 in *Cyparium*) are consistently in a membrane while spiracles 1-3 among members of the outgroup are all contained within sclerotized paratergites. Character state (1) is absent in the outgroup taxa and it is, therefore, inferred as apomorphic. This character is not observed in specimens *Euscaphidium*, *Cerambyciscapha*, and *Kathetopodion*.

47. NUMBER OF ABDOMINAL SPIRACLES. (0) 8; (1) 2 or 3. Among most members of the Scaphidiinae, the number of abdominal spiracles has been reduced to three or two in

members of *Cyparium*. In some taxa (e.g., some members of *Scaphium* and *Cyparium*) the spiracles have atrophied, there are no associated air sacs, and they are probably not functional. The number of functional spiracles among species of scaphidiines requires detailed study and we have limited our observations to a small portion of dissected taxa. Reduction of the number of spiracles (1), with respect to the outgroup taxa, is inferred as apomorphic. This character is not observed in specimens *Euscaphidium*, *Cerambyciscapha*, and *Kathetopodion*.

48. ABDOMINAL PARATERGITES ON SEGMENT 3 (Figs 7-9). (0) Present; (1) absent. Reduction of the number of paratergites is complicated and variable. We have probably oversimplified the coding of these character states, indicating only complete reduction of the paratergites: character state (1) indicates their complete absence, in contrast, character state (0) indicates presence of 1 or 2 paratergites. The distribution of the number of paratergites among members of the outgroup and ingroup is given in Table 2. We do not recognize serial homologies among paratergites because the comparisons made among segments reveal that character states between segments do not covary in a consistent way. Therefore we treat each segment separately in this and the following characters. We did not examine the structure of paratergites in specimens of *Cerambyciscapha* and *Euscaphidium*.

49. ABDOMINAL PARATERGITES ON SEGMENT 4. (0) Present; (1) absent. See character 48 and Table 3.

50. ABDOMINAL PARATERGITES ON SEGMENT 5. (0) Present; (1) absent. See character 48 and Table 3.

51. ABDOMINAL PARATERGITES ON SEGMENT 6. (0) Present; (1) absent. See character 48 and Table 3.

52. ABDOMINAL PARATERGITES ON SEGMENT 7. (0) Present; (1) absent. See character 48 and Table 3. This character is coded as polymorphic for the Apateticinae. Variation of this character and lack of phylogenetic information of the outgroup creates uncertainty in determining the polarity of this character.

53. ABDOMINAL TERGITE 7 WITH OBLIQUE LINE. (0) Absent; (1) present. Among members of the Scaphiina, there is an oblique line present on the sixth tergite. This line is absent in some species of *Episcaphium*, and the character is coded as polymorphic for this taxon. Character state (1) is absent among members of the outgroup and it is, therefore, inferred as apomorphic.

54. ABDOMEN. (0) Parallel-sided; (1) narrowed posteriorly. The abdomen among members of the Scaphidiinae, Apateticinae, and Trigonurinae is narrowed posteriorly. Among members of the Piestinae and other oxyteline group taxa, the abdomen is parallel-sided. It is likely that character state (0) is primitive, however, the phylogenetic relationships are not known for the outgroup taxa, and character state (1) may be plesiomorphic. Therefore, polarity of this character is equivocal.

55. LENGTH OF ABDOMINAL STERNITE 3. (0) Equal to that of the remaining sternites; (1) larger than that of the remaining sternites. Among members of the Scaphidiinae, several morphological characters of the abdomen covary; length of abdominal sternites 3 and 7 relatively large, abdomen shortened, and elytra covering most of the abdominal tergites. We code only one of these characters because of the likelihood of character non-independence. Character state (1) is absent in members of the outgroup and it is therefore inferred as apomorphic.

56. ABDOMINAL STERNITE 7. (0) Without oblique line; (1) with oblique line. Among members of the Scaphidiina, *Ascaphium*, and some species of *Episcaphium*, there is an oblique line present on the fifth sternite. This character is coded as polymorphic for *Episcaphium*. This feature should not be confused with the line produced by the overlap of tergite onto sternite. Character state (1) is absent among members of the outgroup and it is, therefore, inferred as apomorphic.

57. PROCOXA (Figs 4-6, 15, 16). (0) Transverse; (1) conical. The procoxa of Scaphidiinae are conical and projecting and the trochantin has become fused to the internal wall of the prothorax. In contrast, the procoxa among members of the outgroup is transverse and the trochantin is clearly visible in ventral view. Character state (1) is absent in members of the outgroup and it is inferred as apomorphic.

58. MESOTROCHANTIN. (0) Exposed in ventral view; (1) absent. Among members of the outgroup, the mesotrochantin is clearly visible and articulates with the mesocoxa. Among members of the Scaphidiinae the trochantin appears absent or its location enigmatic. There appears to be no trace of the trochantin on the mesocoxa, where it may have become fused with it; although, it is likely that the trochantin has become fused to the coxa and fusion has become so complete that evidence of the trochantin is no longer visible.

Another possibility is that the mesotrochantin has become fused to the mesosternum. On the mesosternum there is a feature that has been referred to in the past as the "mesepimeron" (see LESCHEN & *al.* 1990), which is an elongate sclerite located adjacent and parallel to the meso-metasternal suture, and has been confused with the true mesepimeron (A.F. Newton, personal communication). This sclerite may be marked internally by a ridge in some of the larger species of Scaphidiinae or not in some smaller species. In addition, the line that marks the sclerite externally may be completely absent in some members of the Scaphisomatini. The "mesepimeron" may be the trochantin that has become incorporated into the mesosternite.

Regardless of the phylogenetic history of the trochantin, character state (1) is absent in members of the outgroup and it is, therefore, inferred as apomorphic.

59. TIBIAL STRIA (Fig. 11). (0) Absent; (1) present. Members of the Scaphidiina, *Ascaphium*, and *Episcaphium* have striae that run along the entire length of all the tibiae. This feature also occurs in members of the Apateticinae. Because the presence of character state (1) is in part of the outgroup, the polarity of this character is uncertain.

60. TIBIAL SPINES (Figs 28, 29). (0) Present; (1) absent. Well-developed spines distributed along the shaft of the tibia are present in members of the outgroup and *Cyparium*. The remaining members of the Scaphidiinae do not have well-developed spines on the tibia, only the presence of setae. Character state (1) is absent in the outgroup and it is therefore inferred as apomorphic.

61. ABDOMINAL STERNITE 8 WITH ANTERIORLY PROJECTING PROCESS. (0) Absent; (1) present. Among members of *Cyparium* and *Scaphium*, there is a process arising from the anterior edge of the eighth sternite, which may serve as an attachment point for musculature. This process is not found among members of the outgroup, therefore character state (1) is inferred as apomorphic. This character is not observed in specimens of *Kathetopodion*.

62. ABDOMINAL STERNITE 9 OF MALE WITH WELL-DEFINED SCLEROTIZED RIM THAT IS CONTINUOUS ANTERIORLY (Fig. 39). (0) Absent; (1) present. The abdominal ninth sternite of male specimens of Scaphidiinae is a tongue-shaped sclerite that has a well-defined sclerotized rim and is continuous about the anterior apex: the anterior apex is evenly arcuate. The form of the sternite is variable among members of the outgroup, and differ in form from that present among members of the Scaphidiinae. Members of the Apateticinae have the anterior apex separated into two lobes, and are not connected anteriorly. Among members of the Piestinae, the anterior apex is lyreform, and connected at the apex by a membrane. In specimens of *Trigonurus*, the apex is produced into two broad processes that are well-sclerotized. The primitive condition of the ninth sternite of males in the oxyteline group is unknown, however we consider that the form exhibited among members of the Scaphidiinae is substantially different from that occurring among the outgroups, and, therefore, character state (1) is inferred as apomorphic. Male specimens of *Kathetopodion* are unknown.

63. ABDOMINAL STERNITE 10 OF MALE NARROWED ANTERIORLY FORMING A STYLE-LIKE PROCESS. (0) Absent; (1) present. The tenth sternite of male specimens of Scaphidiinae is relatively narrow with the anterior portion produced into an elongate style-like process. Among members of the outgroup the anterior portion of the tenth sternite is not produced into a narrow process and is broadly arcuate or slightly constricted. Character state (1) is absent among members of the outgroup and it is, therefore, inferred as apomorphic. Male specimens of *Kathetopodion* are unknown.

64. ORIENTATION OF THE APEX OF AEDEAGUS. (0) Posteriorly; (1) ventrally. The apex of the median lobe of the aedeagus among members of the Scaphidiina is bent down towards the ventral portion of the aedeagus (in some taxa the aedeagus has rotated 90° from its original position in the abdomen). Among members of the outgroup and the remaining scaphidiine taxa, the median lobe of the aedeagus is directed posteriorly. Character state (1) is absent among members of the outgroup and it is considered apomorphic. Male specimens of *Kathetopodion* are unknown.

65. INTERNAL SAC BENEATH THE PENIS VALVES. (0) Exposed; (1) hidden. Among members of the Scaphidiina the internal sac is concealed beneath the lobes of the penis valves and can only be seen in cleared specimens. Among members of the outgroup the ejaculatory duct is exposed suggesting that character state (1) is apomorphic. Male specimens of *Kathetopodion* are unknown.

66. SCLERITES OF INTERNAL SAC OF AEDEAGUS. (0) Asymmetrical; (1) symmetrical. Among members of the Scaphidiina, exclusive of *Cerambyciscapha*, the internal sac of the aedeagus contains bilaterally symmetrical sclerites. Among members of the remaining Scaphidiinae and the outgroups, the internal sacs of males have asymmetrical sclerites. Character state (1) is absent in the outgroup and it is, therefore, inferred as apomorphic. Male specimens of *Kathetopodion* are unknown.

67. COMPRESSOR PLATE OF AEDEAGUS DISTINCT BEYOND LEVEL OF THE ARTICULATIONS OF THE PARAMERES. (0) Not distinct beyond level of the articulations of the parameres; (1) distinct beyond the level of the articulations of the parameres. Among members of the Scaphidiina the compressor plate of the aedeagus is large and distinct. Among members of the outgroup taxa the compressor plate does not extend beyond the level of the articulations of the parameres and, therefore, character state (1) is inferred as apomorphic. Male specimens of *Kathetopodion* are unknown and this character is coded as unknown in *Cerymbiscapha*.

68. GONOCOXITE IN CROSS-SECTIONAL VIEW. (0) Flattened; (1) rounded. The form of the gonocoxite among members of the outgroup is flattened in cross-section. In contrast, the form of the gonocoxites among members of the Scaphidiinae is rounded in cross-section. Character state (1) is absent in the outgroup and is, therefore, inferred as apomorphic. This character is not observed in the specimens of *Kathetopodion*, *Euscaphidium* and *Cerambyciscapha*.

69. GONOSTYLE (Figs 35-38). (0) Short; (1) long. Among members of the Scaphisomatini and the outgroup, the gonostyle is less than 3 times as long as wide (Figs 36, 37). Among members of *Cyparium*, *Ascaphium*, and *Episcaphium*, the gonocoxite is 3 times as long as wide. Character state (1) is absent among the outgroup taxa and it is inferred as apomorphic. This character is not observed in the specimens of *Kathetopodion*, *Euscaphidium* and *Cerambyciscapha*.

TABLE 1

Old and newly proposed classifications of the Scaphidiinae based on NEWTON and THAYER (1992) and this study.

Current Classification	Proposed Classification
CYPARIINI Achard, 1924	CYPARIINI Achard, 1924
HETEROSCAPHINI Achard, 1914	SCAPHIINI Achard, 1924
SCAPHIDIINI Latrielle, 1807	SCAPHIDIINI Latrielle, 1807
CERAMBYCISCAPHINA Pic, 1915	SCAPHISOMATINI Casey, 1894
DIATELIINA Achard, 1924	HETEROSCAPHINA Achard, 1914
SCAPHIDIINA Latreille, 1807	BAEOCERIDIINA Achard, 1924
SCAPHIINA Achard, 1924	BAEOCERINA Achard, 1924
SCAPHISOMATINI Casey, 1894	SCAPHISOMATINA Casey, 1894
BAEOCERIDIINA Achard, 1924	TOXIDIINA Achard, 1924
BAEOCERINA Achard, 1924	
SCAPHISOMATINA Casey, 1924	
TOXIDIINI Achard, 1924	

TABLE 2

Number of sclerotized paratergites present in the abdomen among members of the Scaphidiinae and taxa used as outgroups. Specimens of *Euscaphidium* and *Cerambyciscapha* were not examined.

Abdominal segment	3	4	5	6	7
Number of paratergites					
Scaphidiinae					
<i>Ascaphium</i>	0	2	2	2	0
<i>Episcaphium</i>	0,1	2	2	2	0
<i>Scaphium</i>	2	2	2	2	0
<i>Scaphidium</i>	0	0	0,1	1	0
<i>Diatelium</i>	0	1	1	1	0
<i>Cyparium</i>	2	2	2	2	0
<i>Kathetopodion</i>	0	0	0	0	0
Scaphisomatini	0	0,1	0,1	0	0
Outgroup taxa					
<i>Apatetica</i>	2	2	2	1	0
<i>Nodynus</i>	2	2	2	2	1
<i>Siagonium</i>	2	2	2	2	1
<i>Zirophorus</i>	1	1	1	1	1
<i>Trigonurus</i>	1	1	1	1	1

TABLE 3

Data matrix used for the cladistic analysis of Scaphidiinae. Character numbers correspond to those mentioned in the text. An * indicates a character state coded as a polymorphism.

	Characters						
	1 1234567890	2 1234567890	3 1234567890	4 1234567890	5 1234567890	6 1234567890	7 1234567890
Ascapium	1111101110	0110111111	1101110010	1101110111	0111011100	0111111111	011000011
Episcaphium	1111101110	011°111**1	11011110*0	*1011*0111	0111011100	01*11*1111	011000011
Scaphium	1111101110	0100111100	1101111010	1101110111	011*011000	0111101101	111000010
Euscapidium	1111111120	01111?1111	1101110021	01?10011??	1111??????	??01111111	0111111??
Scaphidium	1111111120	011110111*	110111*021	0111*01110	1111111111	0101111111	011111100
Cerambyciscapha	1111111010	01111??111	1101110021	01110011??	0111??????	??01111111	011110???
Diatelium	1111111120	01121?1011	1101110021	0111001110	0111111100	0101111111	011111100
Cyparium	1111101100	0101101000	1111110020	1101110111	0101011000	0101101100	111000001
Kathetopodion	1100011121	11011?0100	1111210110	01?000?1??	?101???111	1101101101	??????????
Scaphisomatini	111*1111**	*1*11****0	11112101*0	**0***0*1*	01**111111	11°1101101	011000010
Piestinae	0001000100	0000°00000	1000000000	000100000*	0011000000	0000000000	000000000
Apateticinae	0000000000	0000000000	*000000000	100*000000	0000000000	0*01000010	000000000
Trigonurinae	0000000000	0000000000	0001000000	0000000000	0000000000	0001000000	000000000

RESULTS AND DISCUSSION

Cladistic analysis that used a generalized outgroup (GENGROUP) resulted in one most parsimonious cladogram (Fig. 40) with the following characteristics: TL = 90, CI = 0.744, and RI = 0.736. Cladistic analysis of the Scaphidiinae that used all three outgroups (ALLGROUP) simultaneously to polarize characters in the PAUP runs resulted in one cladogram (Fig. 41B) with the following characteristics: Tree length (TL) = 104, Consistency index (CI) = 0.702, Retention index (RI) = 0.806. Fig. 40 shows the most parsimonious cladogram resulting from GENGROU analysis with the distribution of all the characters used in the analysis.

Among those characters with uncertain polarity assignments in the character analysis those for which the polarity is opposite of that originally proposed are characters 4, 8 (an autapomorphy for *Cerambyciscapha*), and 34 (when ALLGROUP and GENGROU are used), and characters 31 and 40 (when GENGROU is used). The polarity of character 43 remains equivocal in all analyses. Characters 21, 44, and 54 are uninformative regardless of outgroup specification and characters 15, 24, 52, and 54 are uninformative in the analysis that used GENGROU (exclusive of those characters that occur as synapomorphies of Scaphidiinae).

Regarding the choice and formulation of outgroup taxa, it is, of course, the best option to have a well-defined sister taxon and outgroup structure for polarizing the characters of the ingroup (MADDISON & *al.*, 1984; NIXON & CARPENTER, 1993). However, some putative synapomorphies can be uninformative when specifying a generalized outgroup. For example, some potentially important synapomorphies (characters 15, 24, and 54) for the Scaphidiinae were uninformative when GENGROU was used because these characters are distributed in the basal portion of the cladograms and are codified as uncertain in the outgroup. On the other hand, putative synapomorphies

distributed higher in the cladogram (e.g., characters 34, 43, and 59) are not affected by ambiguous polarity in the analysis using GENGROUP.

The number of paratergites among the Scaphidiinae is very variable, suggesting that this set of characters is weak in their phylogenetic information. Also, we may have oversimplified the coding and homologies of the paratergal character states. Therefore, we investigated the performance of these characters in the cladistic analyses. If characters 48 - 52 (see character analysis) are removed from the data matrices, and the analyses repeated, the same topologies as that in Figs 40 and 41 are produced regardless of type of outgroup. On the basis of these analyses the paratergal characters do not affect the relationships among the tribes and subtribes.

Among the two topologies of the cladograms produced by the above analyses, there is strong evidence that most family group taxa are monophyletic. However, the Scaphidiini (including the Cerambyciscaphina, Diateliina, Scaphiina, and Scaphidiina) are paraphyletic with respect to the placement of the Cypariini and Scaphisomatini (including *Kathetopodion*), and with respect to each other (Fig. 41). The phylogenetic placement of the Cypariini is somewhat enigmatic. It is either placed at the base of the Scaphidiinae, as sister taxon of the remaining members of the subfamily, or forms a clade with members of Scaphidiina.

On the basis of the consistent patterns revealed by the phylogenetic analyses discussed above we make the following changes in the higher classification of the Scaphidiinae. We elevate the subtribes Scaphiina and Scaphidiina to tribal status, and the monotypic subtribes Cerambyciscaphina and Diateliina included in the Scaphidiina are eliminated, such that *Cerambyciscapha* and *Diatelium* are placed into the Scaphidiini.

LESCHEN (1993) proposed relationships for North American genera of Scaphidiinae based upon larval and adult characters. Three trees that were produced from his study exhibit similar conflicts among relationships for representatives of the Cypariini, Scaphidiini, and Scaphiini, although the Scaphisomatini were always placed as a derived taxon. Adequate tests for the relationships proposed in this study can be made by additional information gathered from other characters that may be useful for phylogenetic reconstruction. Therefore it is necessary to procure more larval and adult material, and information from live specimens (fungal hosts, habitats, mating behaviours, etc.) and add this information to our data set to test the phylogenetic hypotheses we propose.

TRIBE SCAPHIINI

The Tribe Scaphiini is monophyletic based on the presence of two unambiguous synapomorphies: endocarina at base of head present along half of the length of the gular region (16) and abdominal tergite 7 with an oblique line (53). Two characters supporting this clade are: head with a neck (14) and presence of a transverse mesosternal ridge (27).

The sister relationship between *Ascaphium* and *Episcaphium* is well supported by several characters (Fig. 40).

TRIBE SCAPHIDIINI

The tribe Scaphidiini is well supported in our analysis by the following unambiguous synapomorphies: eye notched (13), posterior angle of the prothorax molded onto the anterior angle of the elytron (19), presence of a basal stria on the pronotum (20), mesothorax with an anterior process (30), metasternum with a median longitudinal line (33) and male setiferous sex patch (37), abdominal sternite with an oblique line (56), presence of tibial striae (59), apex of aedeagus oriented ventrally (64), and internal sac hidden beneath penis valves (65). Concordant with these characters are the width of mesosternal process more than that of mesocoxa (29-2), compressor plate of aedeagus distinct beyond level of articulation of the parameres (67), and gonocoxite flattened in cross-sectional view (68-0).

The relationships among the genera of Scaphidiini are supported by relatively few characters, although the sister relationship between *Euscaphidium* and *Scaphidium* is supported by one unique unreversed character (presence of prescutal stridulatory files in males (41)). Likewise, *Diatelium* is sister taxon of these based on a unique and unreversed character (internal sclerites of the aedeagus symmetrical (66)). Because so few specimens of *Euscaphidium* and *Cerambyciscapha* are available for study and these are known only from one sex, many characters were scored as unknown in the data matrix. The discovery of additional specimens of these will provide useful data that will fill gaps in our knowledge of certain character states and ultimately test the relationships we proposed in this study.

TRIBE SCAPHISOMATINI

The tribe Scaphisomatini is the largest family group taxon among Scaphidiinae and the relationships among its members are largely unknown. There is adequate data that suggest that *Kathetopodion* is a member of this tribe based on four unambiguous synapomorphies: prosternum in front of coxa reduced to length shorter than that of procoxa (23), procoxal cavities internally closed by the fusion of the prosternum and hypomeron (25-2), mesosternum with an anvil-like process (28), and abdominal paratergites absent from segment 6 (51). Concordant with these characters are: mandible with one tooth on the incisor lobe (4-0), antennomeres 3-11 asymmetrical (10), shape of mentum wider than long (17-0), premetacoxal lines present on metasternum (34-0), and epipleuron in lateral view oblique (43-0). These characters are variable among members of Scaphisomatini and whether these are truly synapomorphies will only be determined by a detailed cladistic analysis of the tribe at the generic level.

TRIBE CYPARIINI

The monogeneric tribe Cypariini is supported by the following unambiguous synapomorphies: prosternum in front of procoxae reduced to a length less than that of procoxa (23), abdominal sternite 8 with anteriorly projecting process (61), and gonostyle long (69). Concordant with these is the width of the mesosternal process more than that of mesocoxa (29-2).

KEY TO THE GENERA OF THE SCAPHIDIINAE, EXCLUDING THE SCAPHISOMATINI

1. Antennal segments 3 to 11 filiform and/or flattened and asymmetrical, usually smaller species. Scaphisomatini
- Antennal segments not filiform, symmetrical, usually larger species. 2
2. Antenna with antennomeres of club round and compact (Fig. 14). 3
- Antenna with antennomeres of club flattened and loose. (Scaphidiini) 6
3. Anterior portion of prosternum reduced (Figs 15, 31), smaller than 1/3 width of coxa, pro- and mesotibia with conspicuous raised spines (Figs 28, 29). (Cypariini) *Cyparium*
- Anterior region of prosternum prolonged (Fig. 16), longer than 1/3 coxal width, pro- and mesotibia without conspicuous spines. (Scaphiini) 4
4. Eyes entire not emarginate, metatarsus with tarsomere 1 about as long as 2. *Scaphium*
- Eyes emarginate, metatarsus with tarsomere 1 much longer than 2. 5
5. Mesosternal ridge present (Fig. 12). *Episcaphium*
- Mesosternal ridge absent. *Ascaphium*
6. Antenna elongate, longer than length of body. *Cerambyciscapha*
- Antenna shorter than length of body. 7
7. Neck present and elongate (Fig. 1). *Diatelium*
- Neck absent. 8
8. Posterior angle of prothorax strongly extended and pointed, lateral margin of prothorax strongly sinuate, anterior region of elytra rugose (Fig. 1a) *Euscapidium*
- Posterior angle of prothorax not strongly extended and pointed, lateral margin of prothorax not sinuate, elytra not rugose. *Scaphidium*

CYPARINI Achard, 1924

Cypariini Achard, 1924

Type genus: *Cyparium* Erichson, 1845**Cyparium** Erichson, 1845

(Figs 13-15, 28, 29, 31, 35)

Type species: *Cyparium palliatum* Erichson, 1845, by monotypy.*Yparicum* Achard, 1920. Type species: *Yparicum yunnanum* Achard, 1920, by monotypy. Synonymy by Löbl (1992).

DESCRIPTION. - Length 2.5-6.5 mm. Hypopharynx with scattered pores, microtrichia composed of equal sizes. Terminal labial palpus not inserted subapically into penultimate palpus. Galea without subapical short bristles, galeal process not well-developed. Labral setae thickened. Antenna (Fig. 14) not filiform, antennomeres of club rounded and compact. Scrobal setae 4. Eye not emarginate. Head not prolonged beyond eyes, without distinct tempora. Gular carina distinct along length of suture. Proventriculus with 6 rods, setae not observed. Pronotum with posterior angle pointed, loosely

pressed to sides of elytra, sub-basal stria absent. Anterior portion of prosternum greatly reduced. Mesosternal ridge (Fig. 13) present. Mesocoxal cavities separated by more than coxal width. Process on prepectus absent. Submesocoxal lines (Fig. 13) connected. Longitudinal line on metasternum present. Metacoxae transverse. Intermetacoxal plate present. Metasternal setae present. Male metasternum without setose patch. Metasternum without paired impressions, costae or tubercles. Metendosternite constricted beyond point of anterior tendon attachment, basal piece carinate dorsally. Male without prescutal files. Epipleuron slightly horizontal. Posterior margin of elytra serrate. Elytral interlocking mechanism of the tongue-in-groove type. Wing vein 3 absent, vannal lobe absent. Spiracles 4-8 absent or nonfunctional, abdominal spiracle 3 not in membrane. Oblique line of abdominal sternite 7 absent. Femora and tibia with spines.

Male. - Metasternite with paired intermetacoxal processes in some species. Abdominal sternite 9 with anterior process. Aedeagus resting on its side, apex bent downwards, orifice exposed, valves overlapping, with three well-developed lobes of the median lobe, internal sac without complex symmetrical sclerites, compressor plate not distinct.

Female. - Coxite (Fig. 35) flattened in cross section, with lateral long setae. Style elongate without 2 long apical setae.

Comments. - The 48 species of *Cyparium* are relatively homogenous in external and aedeagal characters. Most species are uniform in colour (black or light brown), however, some tropical species are spotted or have apical bands on the elytra. A key to the Asian species is provided by LÖBL (1991). Males of some species have paired processes originating from the posterior margin of the metasternal process.

Distribution. - Almost world wide; Absent from oceanic islands, northern Africa, Australia, Europe, Madagascar, New Guinea and Chile.

Larval descriptions. - *Cyparium sibiricum*, (KOMPANTSEV & POTOTSKAYA, 1987), general description, (NEWTON, 1991).

Biology. - Specimens of adults and larvae have been collected mainly from Agaricales (NEWTON, 1984; KOMPANTSEV & POTOTSKAYA, 1987), but have also been reared from coral fungi (Clavaceae) and tooth fungi (Hydnaceae). Records from coral fungi include the North American species *Cyparium terminale* (from ?*Clavaria*; NEWTON, 1984) and an undetermined Peruvian species (from *Pterula* sp.; Leschen, personal observation). In both instances larvae were present and/or reared. Once *C. terminale* was reared from the fungus *Tremellodendron pallidum*, a persistent coral-like fungus in the Tremellales (LESCHEN, 1988). Larvae feed mainly on the hyphae of these fungi (NEWTON, 1984).

SCAPHIINI Achard, 1924

Scaphiitae Achard, 1924

Type genus: *Scaphium* Kirby, 1837

Description. - Hypopharynx with central pores, setae of equal sizes (Fig. 21). Terminal labial palpus inserted subapically into penultimate palpus. Galea without

subapical setae, galeal process not well developed. Labral setae not thickened. Antenna not filiform, club loose, slightly or not flattened. Scrobal setae 4. Head prolonged beyond eyes with distinct tempora, gular carina distinct basally. Proventriculus with 8 rods and setose. Anterior portion of the prosternum elongate. Pronotal angle usually rounded. Prepectus without process. Male without prescutal files or setal patch. Scutellum 1/3 width of entire mesonotum. Metasternum with single seta, median longitudinal line and male setose patch absent, paired impressions or costae or tubercles present or not. Intermetacoxal plate present (Fig. 16). Metacoxae not strongly transverse. Metendosternite (Fig. 34) carinate basally, dorsal arms not constricted above insertion of anterior tendon. Epipleuron vertical. Elytral interlocking mechanism of the tongue-in-groove type. Abdominal spiracle 3 in membrane. Femora and tibia without spines.

Male. - Aedeagus resting on its side, apex bent downward, orifice not exposed, valves usually overlapping, basal bulb without three sclerotized lobes, internal sacs without complex asymmetrical sclerites, compressor plate not distinct beyond level of paramere articulation.

Female. - Coxite (Fig. 38) cylindrical in cross section, lateral long setae absent. Style elongate, without two long setae.

Ascaphium Lewis, 1893

Type species: *Ascaphium sulcipenne* Lewis, 1893, designated by LÖBL (1992).

Description. - Length 3.5-7.0 mm. Eye emarginate. Antennal club loose, not flattened. Posterior pronotal angle rounded, loosely molded to elytra. Sub-basal stria of pronotum present. Mesosternal ridge absent. Mesocoxal cavities not separated more than coxal width. Submesocoxal lines connected. Elytron with deep stria, posterior edge serrate. Anal vein 3 absent. Spiracles 4-8 absent and/or nonfunctional. Oblique line on sternite 7 absent. Intermetacoxal process of male absent. Male sternite 8 without anterior process. Female coxite without long lateral setae. Metatibia of male not curved. Metatarsomere 1 longer than 2.

Comments. - The 7 known species of *Ascaphium* are uniformly black. The pattern of the elytral stria are important characters for species identification and they can be identified with the key given by LÖBL (1992).

Distribution. - Eastern Palaearctic and southeast Asia.

Biology. - The Japanese species *Ascaphium sulcipenne* and *A. tibiale* have been collected from *Trametes versicolor* and other polypore fungi (T. Nakane, personal communication).

Episcaphium Lewis, 1893

(Fig. 38)

Type species: *Episcaphium semirufum* Lewis, 1893, by monotypy.

Phenoscapium Achard, 1922b. Type species: *Phenoscapium callosipenne* Achard, 1922b, by monotypy. **Syn. nov.**

Description. - Length 4.5-7.0 mm. Eye emarginate. Antennal club loose, flattened. Posterior pronotal angle rounded or not, and tightly molded to elytra. Sub-basal stria of pronotum present. Mesosternal ridge present. Mesocoxal cavities separated by more than coxal width. Submesocoxal lines connected or not. Posterior edge of elytra serrate or not. Wing with vannal lobe and vein 3 absent. Spiracles 5-8 absent and/or nonfunctional. Oblique line of abdominal sternite 7 present or absent. Intermetacoxal process of male absent. Male sternite 8 without anterior process. Female coxite with long lateral setae. Metatibia of males not curved. Metatarsomere 1 longer than 2.

Comments. - Achard (1922b) described the species *Phenoscapium callosipenne*, placing it in a genus separate from *Episcaphium*. He erected this genus based on the antennal club which is not flattened with the segments widened abruptly from the base and the posterior angle of the pronotum pointed and weakly extended behind. Achard also recognized that the elytra are relatively shorter in this species and that the elytral surface is uneven and irregular. We believe that Achard was incorrect in recognizing *Phenoscapium* as a separate genus because the characters he used are either variable (antennal characters and posterior pronotal angle) or autapomorphies (elytral surface irregular). Therefore we place *P. callosipenne* in the genus *Episcaphium*.

Species of *Episcaphium* can be identified with the key provided by LÖBL (1992). The species *E. callosipenne* is not included in this key but can be distinguished by the remaining species by its black colouration, the submesocoxal lines connected at the middle, and by the uneven surface of the elytral disc.

Distribution. - Eastern Palaearctic and southeast Asia.

Biology. - Specimens of *E. semirufum* have been collected from fungus covered rotten logs and from polypores (I. Löbl, personal observation, S.I. Naomi and T. Nakane, personal communications).

Scaphium Kirby, 1837

(Figs 16,21,23,24,26,34)

Type species: *Scaphium castanipes* Kirby, 1837, by monotypy.

Description. - Length 4.5-7.0 mm. Eyes entire. Antennal club loose, antennomeres not flattened. Posterior pronotal angle rounded, not molded tightly onto elytra. Sub-basal stria of pronotum absent. Mesosternal ridge present. Mesocoxal cavities not separated more than coxal width. Submesocoxal lines connected. Posterior edge of elytra with or without serrations. Anal vein 3 present. Spiracles 5-8 absent and/or nonfunctional. Oblique line on abdominal sternite 7 absent. Intermetacoxal process of male present. Male sternite 8 with anterior process. Female coxites with lateral long setae. Metatibia curved in males. Metatarsomere 1 as long as 2.

Comments. - The four species included in *Scaphium* are entirely black in colour. *Scaphium immaculatum* can be distinguished from the other species by its well developed metasternal process in the male which is produced posteriorly into two large flattened processes. Examination of the single type from Paris revealed that the generic

placement of *Scaphium ferrugineum* is certain but that the distribution record from South African is dubious. Males of *Scaphium* have curved tibia and intermetacoxal processes, and in some species there may be paired impressions on the metasternum.

Distribution. - Holarctic, ?South Africa.

Larval descriptions. - *Scaphium quadraticolle*, (KOMANTSEV & POTOTSKAYA 1987); *Scaphium castanipes*, (ASHE, 1984), general description, (NEWTON, 1991).

Biology. - Species of *Scaphium* have been associated with members of Agari-cales (ASHE, 1984; KOMANTSEV & POTOTSKAYA, 1987). NEWTON (in ASHE, 1984) noted that larval specimens that may be members of *Scaphium* from Alaska, had guts filled with fine fungus mycelium.

SCAPHIDIINI Latreille, 1807

Scaphidiina Latreille, 1807

Scaphiitae Achard, 1924

Type genus: *Scaphidium* Olivier, 1790

Cerambyciscaphini Pic, 1915b. Type genus: *Cerambyciscapha* Pic, 1915b. **Syn. nov.**

Cerambycaphini Achard, 1924 (misspelled type genus *Cerambyscapha* Pic, 1915b).

Diateliina Achard, 1924. Type genus: *Diatelium* Pascoe, 1863. **Syn. nov.**

Description. - Hypopharynx (Figs 20, 30) with sensory pores scattered on surface, setae of different sizes. Terminal labial palpus with terminal segment subapically inserted into the penultimate palpus. Galea (Fig. 27) with subapical setae. Labral setae thickened (Fig. 25). Eye emarginate. Antennal club loose and flattened. Head not extended beyond eyes, without distinct tempora. Gular carinae internally distinct throughout. Proventriculus with 8 rods and not setose. Posterior pronotal angles tightly molded to elytra. Anterior portion of prosternum reduced. Mesocoxal cavities separated by a distance more than the coxal width. Prepectus with an anterior process. Submesocoxal lines not connected. Metasternum with a median longitudinal line (not observed in *Euscaphidium*), discal setae absent, never with paired impressions, costae or tubercles. Intermetacoxal plate absent. Metacoxa not very transverse. Metendosternite with dorsal arm constricted beyond point of attachment of anterior tendons, basal piece not carinate dorsally (not observed in *Euscaphidium* and *Cerambyciscapha*). Scutellum about 1/2 width of entire mesonotum. Epipleuron vertical. Posterior edge of elytra serrate. Elytral interlocking mechanism evenly undulate (not observed in *Euscaphidium* and *Cerambyciscapha*). Abdominal spiracle 3 in membrane. Spiracles 4-8 absent and/or nonfunctional (not observed in *Euscaphidium* and *Cerambyciscapha*). Oblique line on abdominal sternite 5 present. Femora and tibia without spines.

Male. - Metasternum with setose patch. Abdominal sternite 8 without anterior process. Aedeagus with apex not bent downward, orifice exposed, valves not overlapping, basal bulb without three sclerotized lobes, compressor plate distinct beyond paramere articulation (latter unclear in *Cerambyciscapha*).

Female - (no data for *Euscaphidium* and *Cerambyciscapha*). Coxite flattened in cross section, not cylindrical, with lateral long setae. Style short with 2 long setae.

Euscaphidium Achard, 1922a

(Fig. 1a)

Type species: *Euscaphidium tuberosum* Achard, 1922a, by monotypy.

Description. - Length 8.0 mm (Sumatran specimen). Galeal process well developed. Antenna not filiform, antennal club flattened, insertion not raised. Scrobal setae 6. Neck not prolonged behind. Pronotum with sub-basal stria present. Lateral pronotal margin sinuate, posterior angle pointed. Prosternum horizontal. Mesosternal keel present, ridge absent. Male with prescutal files. Elytra with lateral humeral lobe. Condition of wing not observed. Mesotibia with curved apical spines. Internal sac of aedeagus with complex symmetrical sclerites. Orientation of aedeagus not observed in this species.

Comments. - Known from two male adult specimens.

Distribution. - Sumatra and Borneo.

Scaphidium Olivier, 1790

(Figs 3,5,8,10-12,17-19,27,30,32)

Type species: *Scaphidium quadrimaculatum* Olivier, 1790, designated by LEACH, 1815.

Ascapidium Pic, 1915a. Type species: *Ascapidium sikorai* Pic, 1915a, by monotypy. **Syn. nov.**

Cribrascaphidium Pic, 1920 (sg.). Type species: *Scaphidium irregulare* Pic, 1920, by monotypy.

Syn. nov.

Hemiscaphium Achard, 1922a. Type species: *Scaphidium striatipenne* Gestro, 1880, by original designation. **Syn. nov.**

Hyposcaphidium Achard, 1922a (sg.). Type species: not designated.

Isoscaphidium Achard, 1922a (sg.). Type species: not designated.

Pachyscaphidium Achard, 1922a (sg.). Type species: *Scaphidium arrowi* Achard, 1920, by original designation.

Scaphidiolum Achard, 1922a. Type species: *Scaphidium basale* Castelnau, 1840, by original designation. **Syn. nov.**

Scaphidopsis Achard, 1922a. Type species: *Scaphidium pardale* Castelnau, 1840, by original designation. **Syn. nov.**

Falsoascaphidium Pic, 1923. Type species: *Scaphidium subdepressum* Pic, 1921, by original designation. **Syn. nov.**

Parascaphium Achard, 1923: Type species: *Scaphidium optabile* Lewis, 1893, by monotypy. Synonymy by LÖBL (1968).

Description. - Length 3.0-11.0 mm. Galeal process present, well-developed. Antenna filiform or not, club flattened, insertion not raised. Scrobal setae 4. Neck not prolonged behind. Posterior pronotal angle pointed, lateral margin not sinuate. Prosternum horizontal. Pronotum with sub-basal stria present or absent. Mesosternal ridge (Fig. 12) present or absent, keel present. Male with prescutal files (Figs 17, 32). Elytron without lateral humeral lobe. Anal vein 3 absent. Mesotarsi with straight apical spines. Aedeagus resting on its side or horizontal. Internal sac with complex symmetrical sclerites.

Comments. - The genera placed by us in synonymy with *Scaphidium* have been previously based upon characters that vary considerably and without well-defined syn- or autapomorphies.

Ascapidium was erected by PIC (1915a) for species occurring in Madagascar and is based on relative lengths of antennal segments 5 and 6, punctuation of the

pronotum and elytra, and the convex form of the elytra. These characters vary within members of *Scaphidium*. Although members of *Ascaphidium* are easily recognized by their strikingly punctate dorsal surfaces, the degree of punctuation varies among its included species and strong punctuation is present in other species of *Scaphidium* that do not occur in Madagascar.

Cribroscaphium - Pic (1920), *Falsoascaphidium* Pic (1923), and *Scaphidiolum* Achard (1922a), were described based upon the relative degree of curvature of the pronotum, striae on the body, form of the antennal club, size of the scutellum, and other characters that either vary considerably among members of *Scaphidium* or are consistent for all members of the genus. Members of these groups do not have characters that readily separate them from other members of *Scaphidium*, although many species of *Scaphidiolum* have strongly narrowed frons.

Scaphidopsis Achard (1922a) was erected for species of *Scaphidium* occurring in South America that mainly have a well-developed pronotal hump and a mesosternal keel. These features are present in many members of *Scaphidium*, and although the relative size of the pronotal hump varies among members of the genus, it is relatively large in the type species *S. pardale* compared to most New World members of the genus.

Members of *Hemiscaphium* were recognized by ACHARD (1922a) mainly by the width of the head, which is larger than that of the anterior portion of the prothorax, and by the relative length of the antenna. This latter feature is variable among members of *Scaphidium*. Members of *Hemiscaphium* are distinct, however, and the relative width of the head is associated with the size of the eyes and anterior width of the pronotum, which is variable among members of *Scaphidium*.

New combinations resulting from the above synonymies are given in the Appendix. *Scaphidium* exhibits notable variation, especially the size of the body and eyes, colouration, pronotal features, elytra punctuation, mesosternal characters, and male secondary sexual characters. Division of the 269 species of *Scaphidium* into natural species-groups will require a thorough analysis of all of the inclusive species and is outside the goals of this paper.

Distribution. - World wide, except for oceanic islands, New Zealand and southern South America.

Larval descriptions. - *Scaphidium amurense* (KOMPANTSEV & POTOTSKAYA, 1987); *S. quadrimaculatum* (KASULE, 1968; KOMPANTSEV & POTOTSKAYA, 1987); general description (NEWTON, 1991).

Biology. - Adult and larval fungal host records were reviewed by NEWTON (1984). Most species of *Scaphidium* are associated with lignicolous fungi, grazing mainly on encrusting hymenomycetes. Observations on Neotropical taxa support these data (Leschen, personal observation).

Adults of *Scaphidium* exhibit a wide degree of variation (large eyes, sexual dimorphism, etc.) which suggests a wide array of adult behaviors. Larval behaviors may also be variable. NEWTON (1984) reported that larvae from an undetermined species in Panama observed on a white resupinate polypore lived in tunnels among the

fungus or wood and emerged at night to feed. LESCHEN (1993a) notes that larvae of another undetermined species from Mexico constructed retreats of frass from which individuals would emerge to feed during the day on the hymenium of an undetermined orange polypore.

Cerambyciscapha Pic, 1915b

(Figs 20, 25, 39)

Type species: *Cerambyciscapha doherityi* Pic, 1915b, by monotypy.

Description. - Length 6.5 mm (known specimen). Galeal process poorly-developed. Antenna filiform without antennal club, insertion raised. Scrobal setae 4. Head not prolonged behind. Posterior pronotal angle pointed. Pronotum with sub-basal stria present, lateral margins not sinuate. Prosternum horizontal. Mesosternal keel absent. Male without prescutal files. Mesosternal ridge absent. Condition of wing not observed in this species. Elytra without lateral humeral lobe. Mesotarsi with straight apical spines. Aedeagus on side. Internal sac without complex symmetrical sclerites.

Comments. - Known from a single male specimen.

Distribution. - Borneo.

Diatelium Pascoe, 1863

(Fig. 1)

Type species: *Diatelium wallacei* Pascoe 1863, by monotypy.

Description. Length 13-20 mm. Galeal process poorly developed. Antennae not filiform, antennal club loose and flattened, insertion not raised. Scrobal setae 10. Head (Fig. 1) prolonged behind eyes. Pronotal angle rounded. Pronotum with sub-basal stria present, lateral margin not sinuate, male with distinct anteriodorsal notch. Prosternum vertical. Mesosternal ridge absent, keel present. Male without prescutal files. Elytra without lateral humeral lobe. Anal vein 3 present. Mesotarsi with straight apical spines. Aedeagus on side. Internal sac with complex symmetrical sclerites.

Comments. - Status of the variety *D. wallacei*, var. *laterale* Achard (1920) is unknown.

Both sexes of *D. wallacei* have elongate necks, but the length of the male neck is usually longer, up to two times the length of the body. Males also differ in the form of the prothorax; the anterior portion of the pronotum is furnished with a notch, the pronotal volume is larger (Fig. 1), and the prosternum is narrow and is vertical in position. A dissection of a male revealed two large tendons that extend from the base of the neck to the sternum near the procoxae.

Distribution. - Borneo, Sulawesi, and Sumatra.

Biology. - Achard (1920) briefly mentioned that *D. wallacei* was collected from fungi growing on a trunk of a tree.

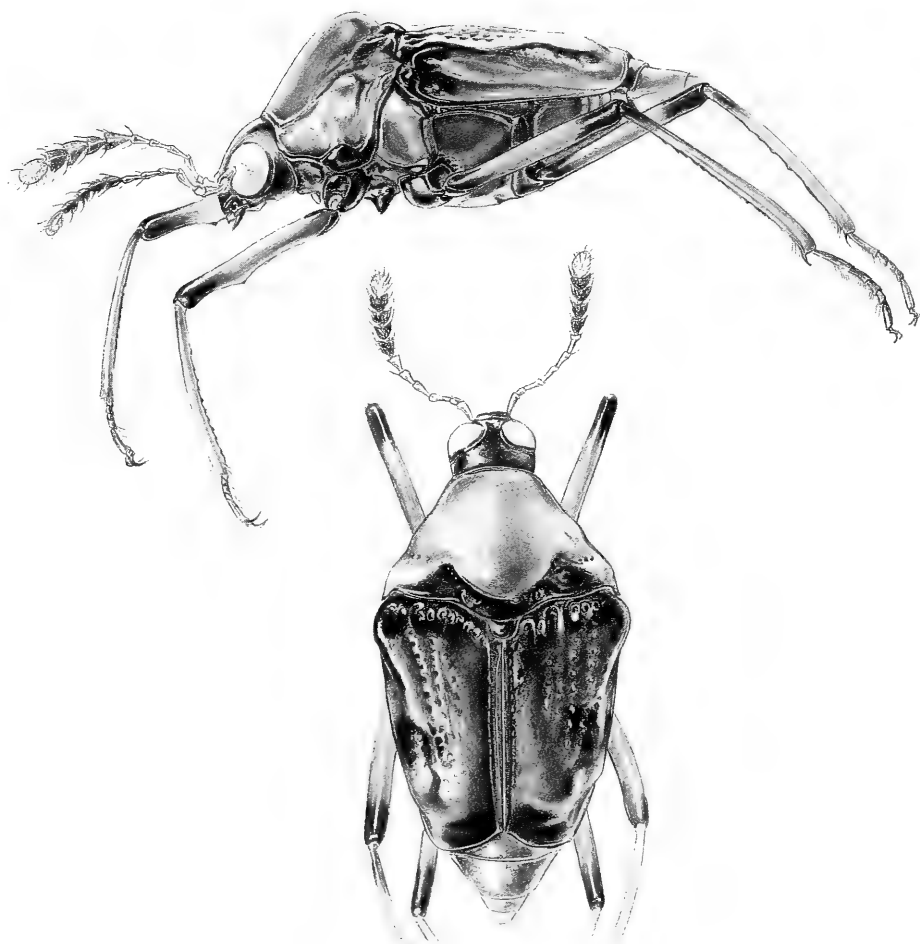
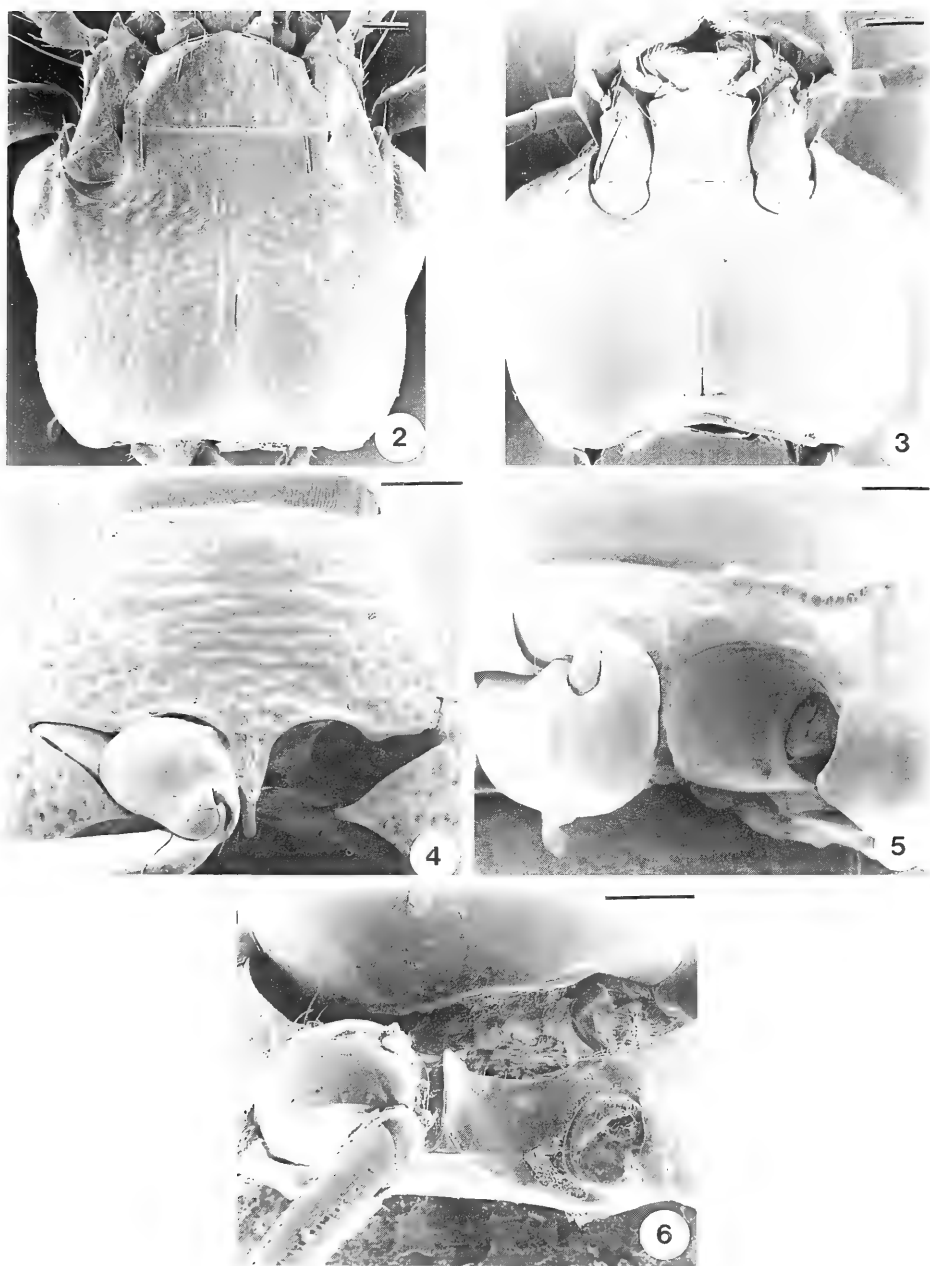


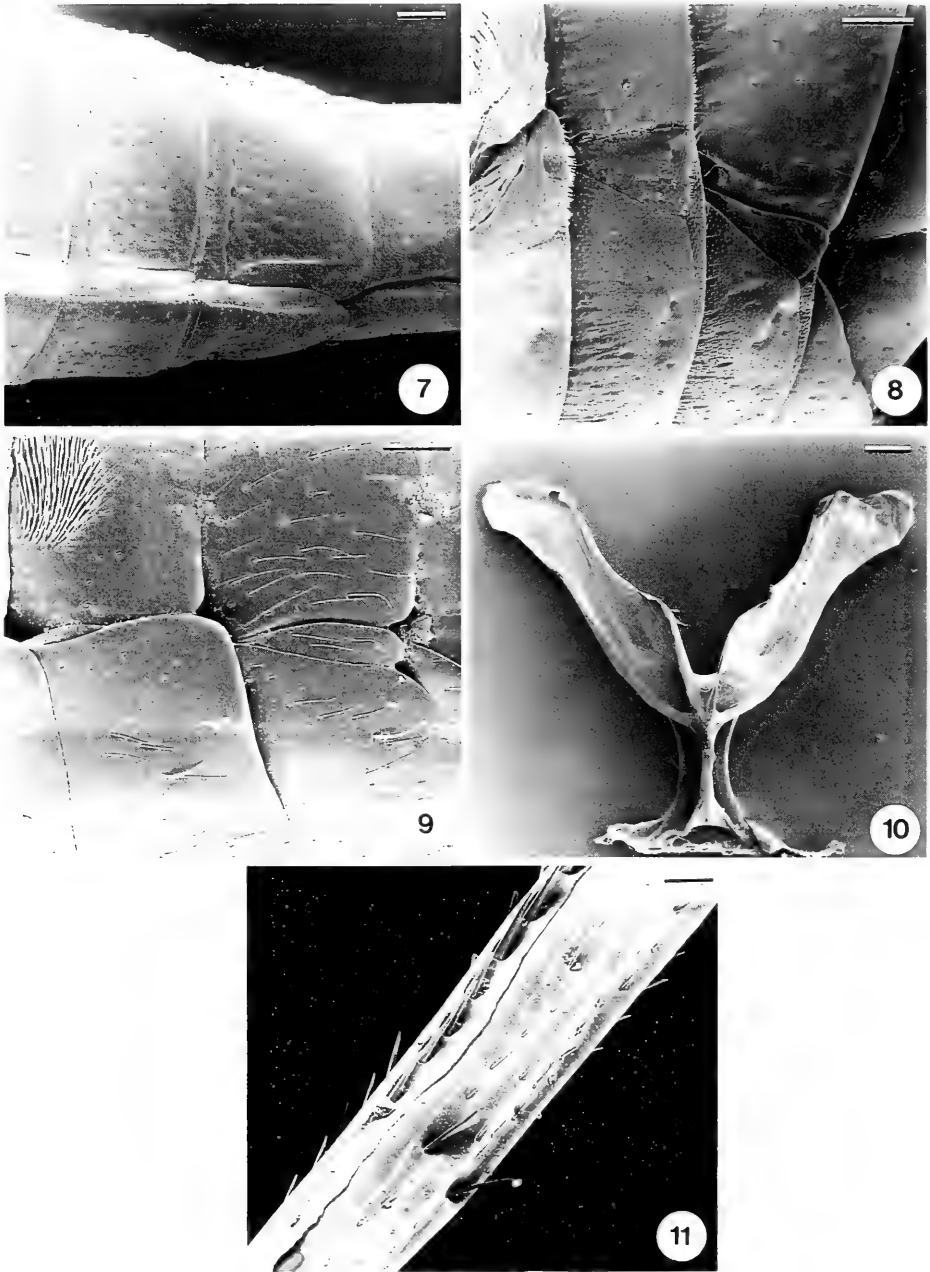
FIG. 1a

Habitus of *Euscaphidium tuberosum*, lateral and dorsal views.



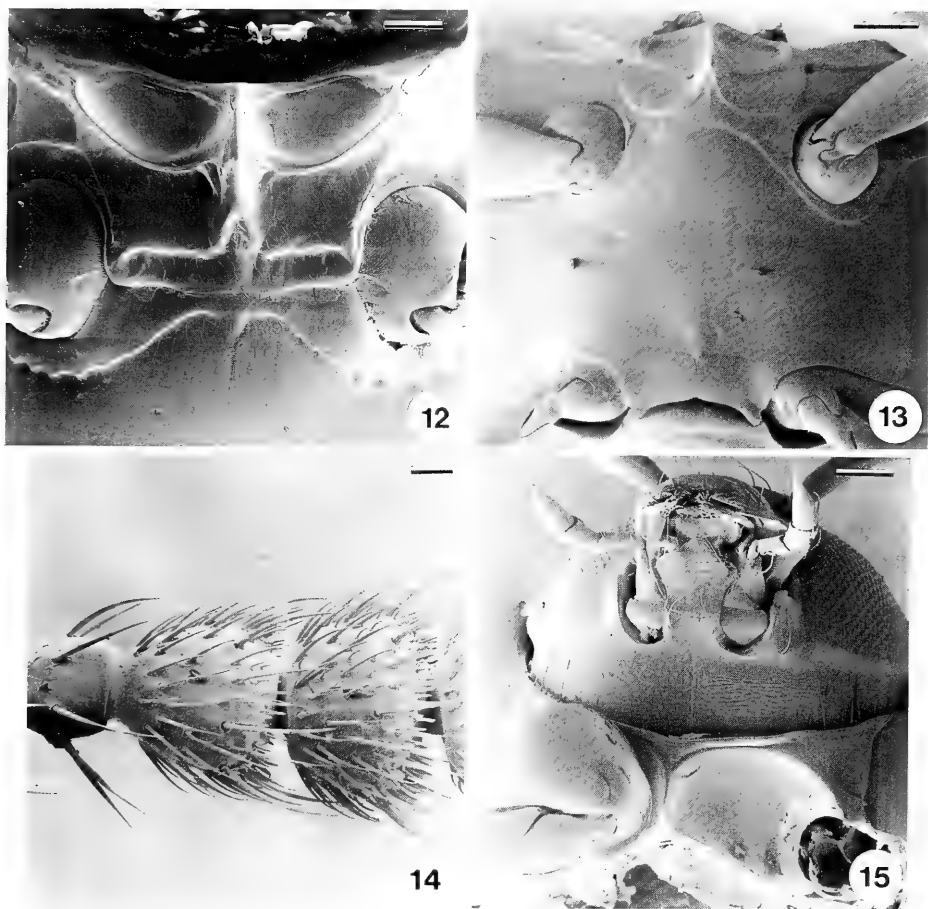
FIGS 2-6

2, *Trigonurus asiaticus*, head, ventral view (scale bar 100 μ m); 3, *Scaphidium quadrimaculatum*, head, ventral view (scale bar 200 μ m); 4, *Trigonurus asiaticus*, prosternum (scale bar 200 μ m); 5, *Scaphidium quadrimaculatum*, prosternum (scale bar 200 μ m); 6, *Scaphisoma agaricinum*, prosternum (scale bar 100 μ m).



FIGS 7-11

7, *Trigonurus asiaticus*, paratergites (scale bar 100 μ m); 8, *Scaphidium quadrimaculatum*, paratergites (scale bar 100 μ m); 9, *Scaphisoma agaricinum*, paratergites (scale bar 50 μ m); 10, *Scaphidium quadrimaculatum*, metendosternite (scale bar 200 μ m); 11, same, portion of metatibia (scale bar 50 μ m).

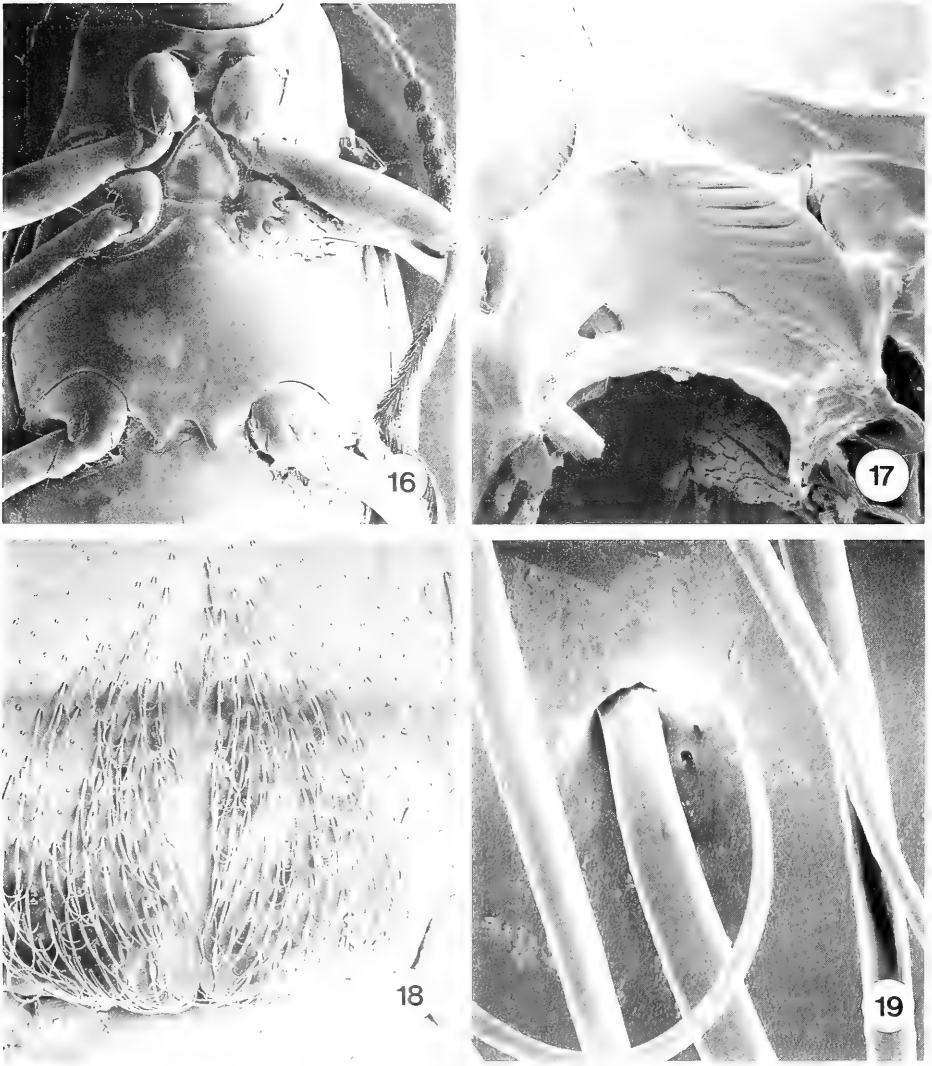


FIGS 12-15

12, *Scaphidium quadrimaculatum*, ventral view of mesonotum; 13, *Cyparium terminale*, ventral view of body; 14, same, ventral view of antenna; 15, same, head and prothorax, ventral view.

ACKNOWLEDGMENTS

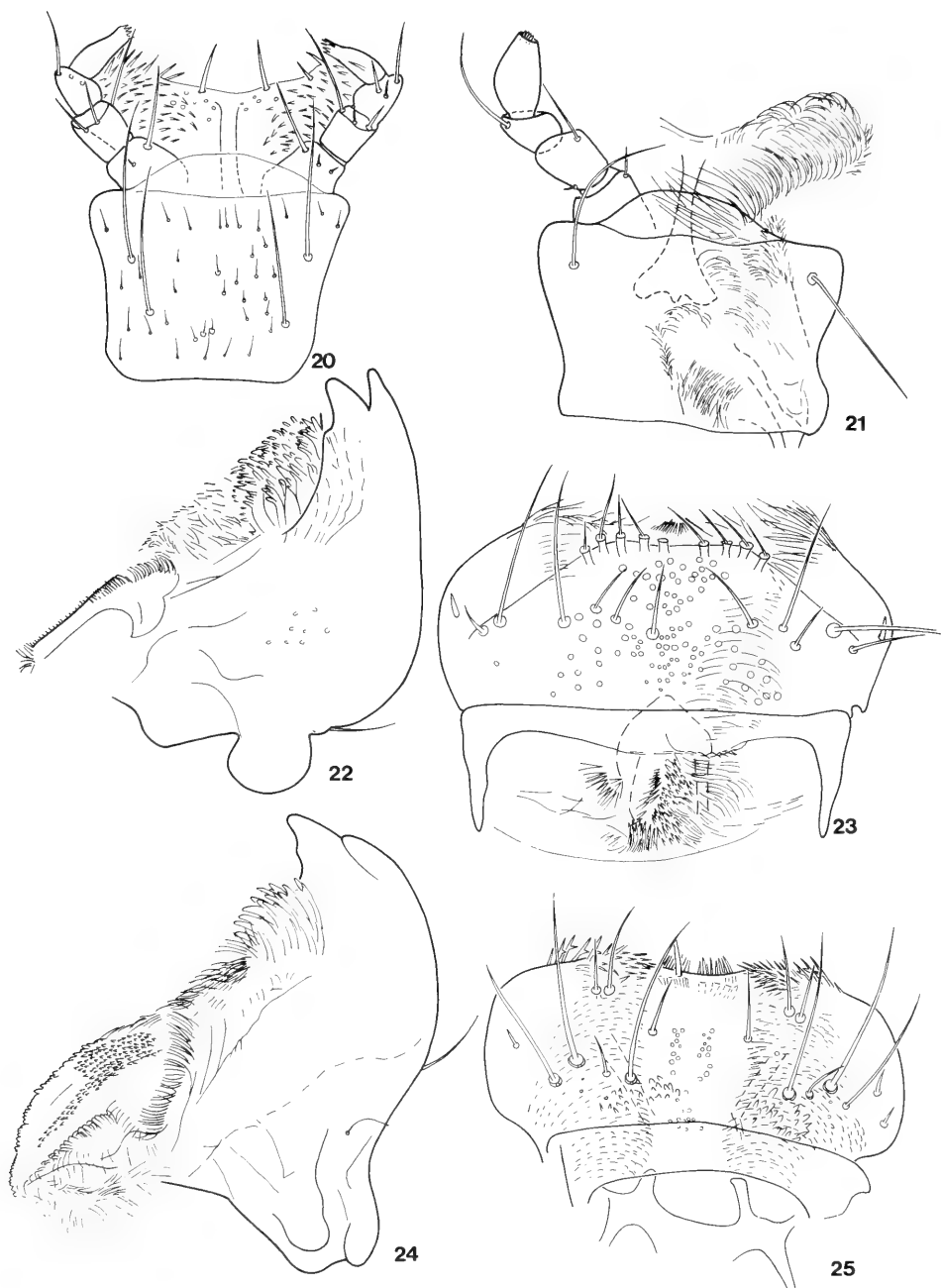
We thank Nicolle Berti, Muséum National d'Histoire Naturelle, Paris, for the loan of the type specimen of *Cerambyciscapha dohertyi*, Roberto Poggi, Museo Civico di Storia Naturale, Genova, for the loan of the type of *Euscaphidium tuberosum*, and Malcolm Kerley, The Natural History Museum, London, for the type of *Kathetopodion borneense*. Additional material for study was kindly supplied by David Kistner, Alfred F. Newton, Shun-Ichiro Naomi, and Steve Ashe. Shun-Ichiro Naomi and Takehiko Nakane provided us with valuable biological information on Japanese species. Scanning electron micrographs were made with the assistance of Bruce Cutler and Jean



FIGS 16-19

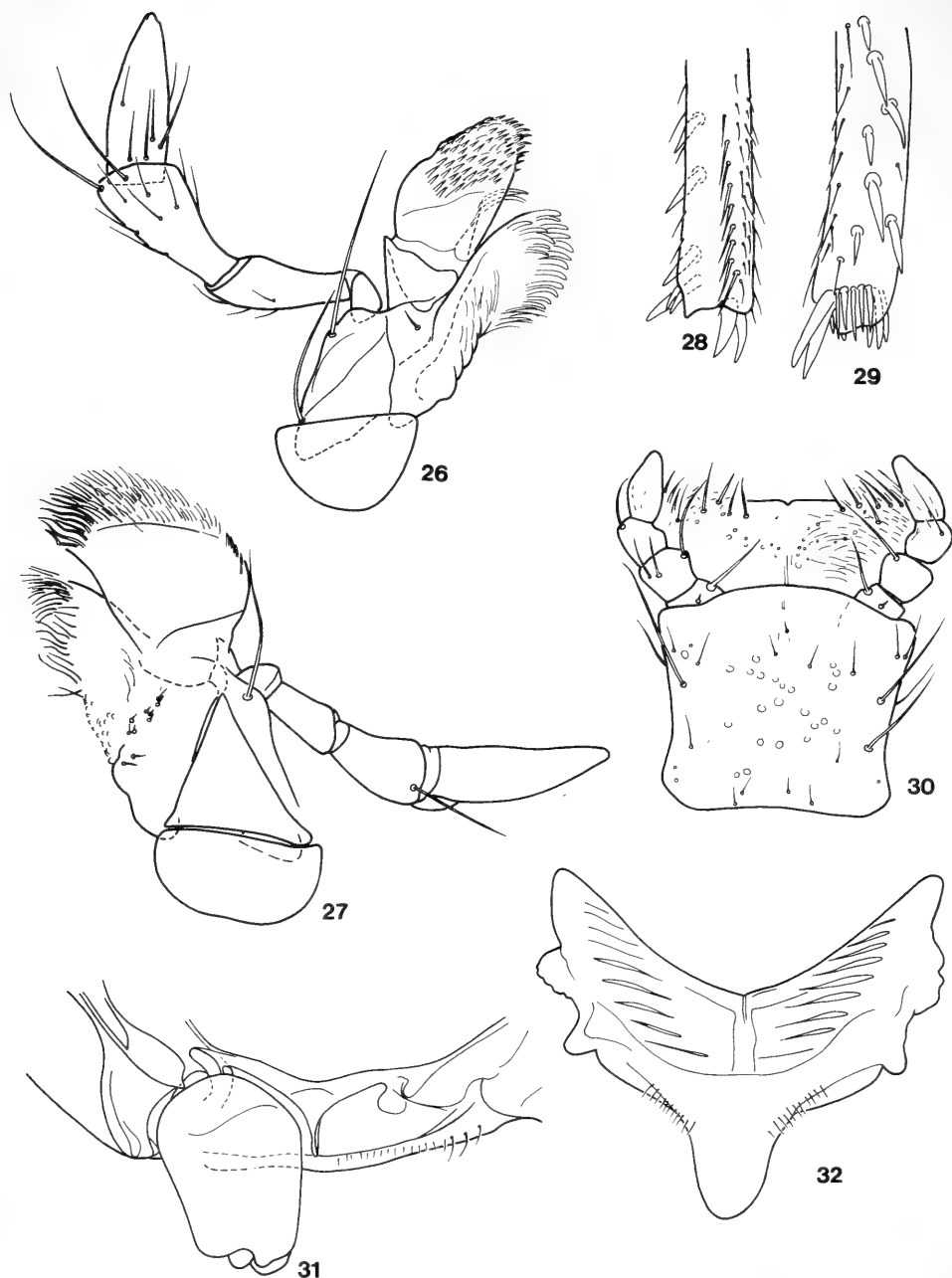
16, *Scaphium immaculatum*, ventral view of male; 17, *Scaphidium quadrimaculatum*, anterior view of mesonotum showing prescutal files of male; 18, same, ventral view of setal patch of male; 19, same, close-up image of the base of a seta part of the male setal patch.

Wüest. The habitus illustration of *D. wallacei* was drawn by Steve Lingafelter. The illustrations of *E. tuberosum* were drawn by Nicolette Lavoyer. This study would not have been accomplished without a two visiting grants to RABL from the Muséum d'histoire naturelle, Geneva. We gratefully appreciate review of this paper by Steve Ashe, and comments by A. F. Newton, Jr. and Daniel Burckhardt.



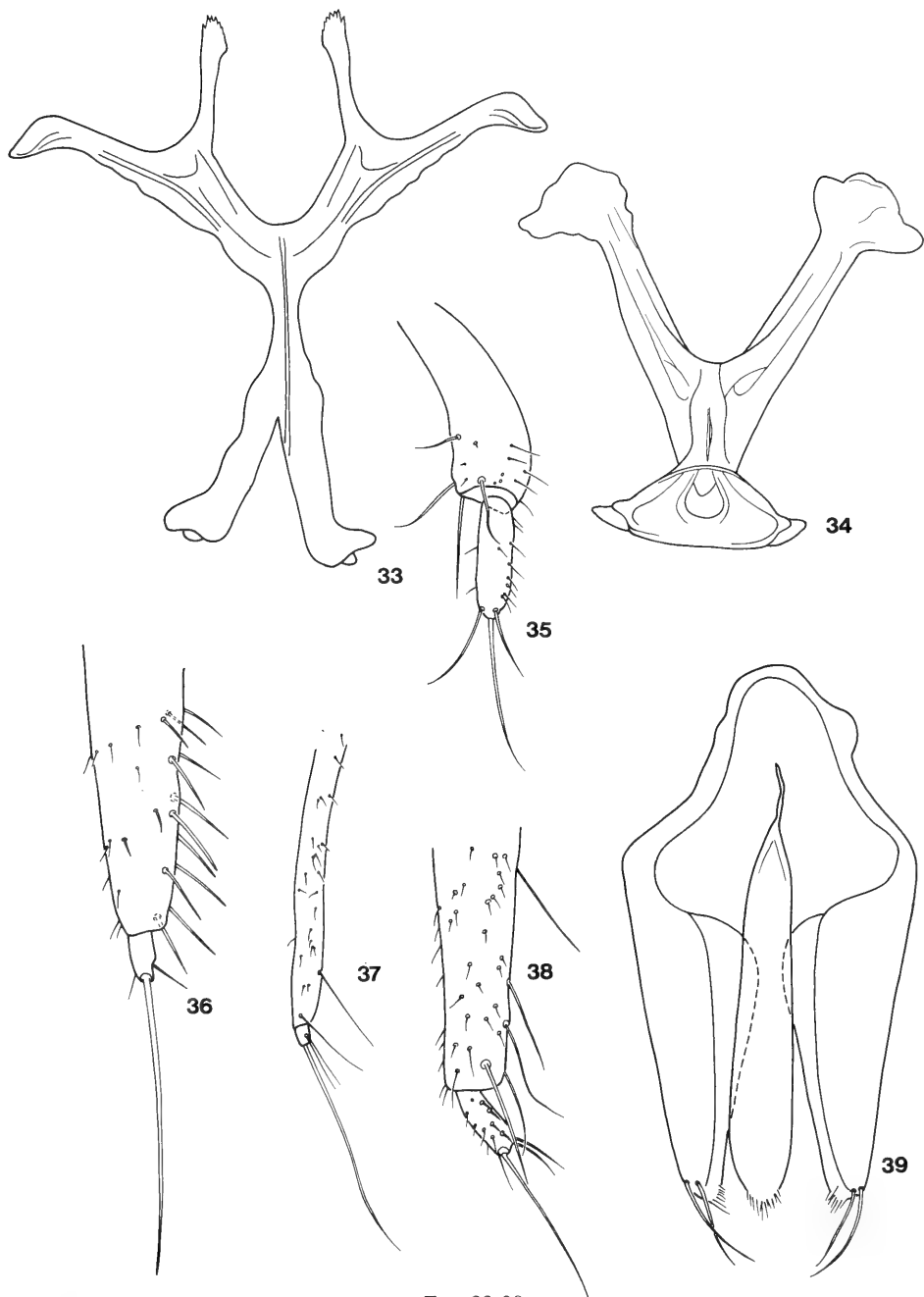
FIGS 20-25

20, Labium of *Cerambyciscapha dohertyi*, ventral view with ghosted image of hypopharynx; 21, *Scaphium immaculatum*, ventral view with ghosted image of hypopharynx; 22, *Scaphidium quadriguttatum*, ventral view of left mandible; 23, *Scaphium immaculatum*, dorsal view of clypeus with ghosted image of epipharynx; 24, same ventral view of left mandible; 25, *Cerambyciscapha dohertyi*, dorsal view of clypeus with ghosted image of epipharynx.



FIGS 26-32

26, *Scaphium immaculatum*, ventral view of right maxilla; 27, *Scaphidium quadriguttatum*, ventral view of left maxilla; 28, *Cyparium* sp., distal region of protibia; 29, same, distal region of mesotibia; 30, *Scaphidium quadriguttatum*, ventral view of labium with ghosted image of the hypopharynx; 31, *Cyparium* sp., ventral view of prosternum with left leg removed; 32, *Scaphidium quadriguttatum*, dorsal view of mesonotum.



FIGS 33-39

33, *Trigonurus asiaticus*, anterior view of metendosternite; 34, *Scaphium castanipes*, anterior view of metendosternite (anterior tendons not shown); 35, *Cyparium* sp., coxite of female; 36, *Nodynus japonicus*, coxite of female; 37, *Pseudobironium lewisi*, coxite of female; 38, *Episcaphium saucineum*, coxite of female; 39, *Cerambyciscapha dohertyi*, ventral view of male abdominal sternites 8 and 9.

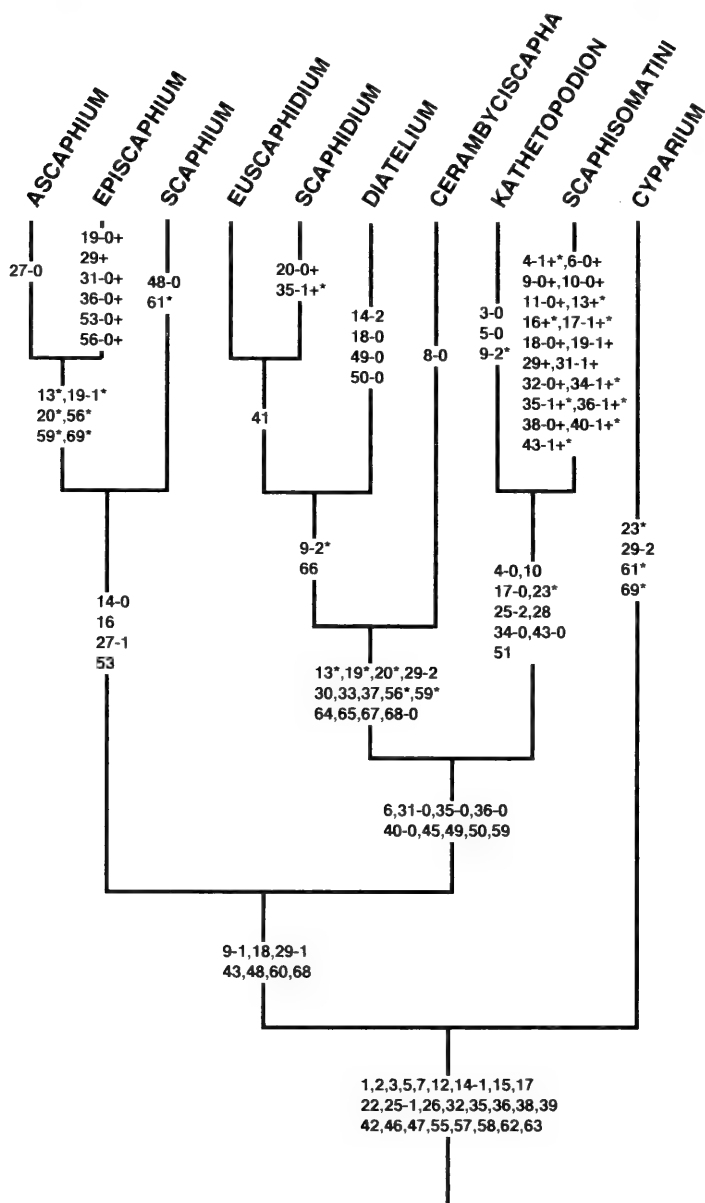


FIG. 40

Cladogram showing the relationships among members of Scaphidiinae. This cladogram was produced by a cladistic analysis using a generalized outgroup to polarize characters. Characters 21, 24, 44, 52, and 54 are uninformative in this analysis and are not mapped onto the cladogram. Homoplasy = *, Polymorphism = +

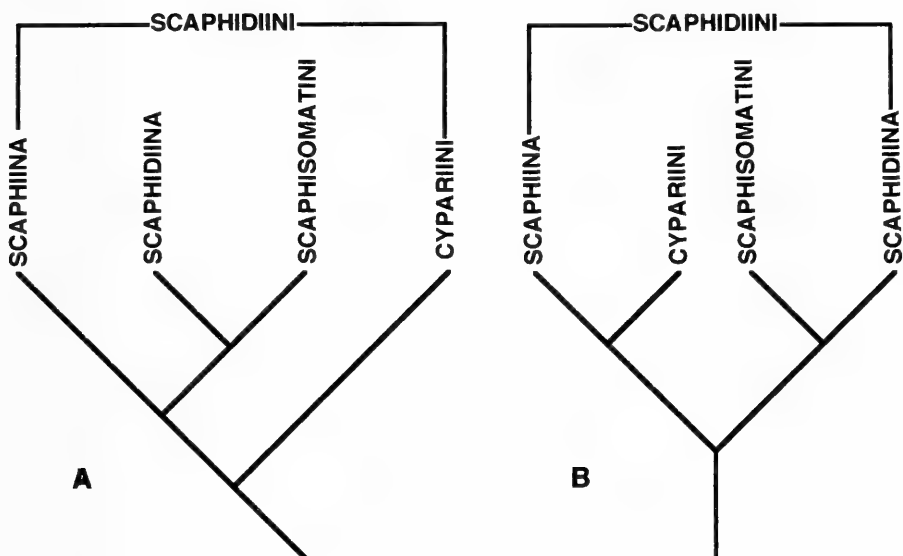


FIG. 41

Two cladograms showing the relationships among members of the higher taxa of Scaphidiinae. Note that Scaphidiini are paraphyletic with respect to the phylogenetic placement of the other tribes.

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APPENDIX: CATALOGUE OF THE CYPARIINI, SCAPHIINI AND SCAPHIDIINI

The list below includes all known published specific and infraspecific names, junior homonyms excepted. Species we have examined for the phylogenetic analysis are indicated by the following signs preceeding the name; (+), dissected species; (-), external and aedeagal characters checked.

Cypariini	
Cyparium	
<i>anale</i> Reitter, 1880	Neotropical
<i>ater</i> Casey, 1900	Nearctic
<i>basilewskyi</i> Pic, 1955	Africa
<i>bowringi</i> Achard, 1922	SE Asia
<i>championi</i> Matthews, 1888	Neotropical
<i>collare</i> Pic, 1920	Neotropical
<i>+concolor</i> (Fabricius, 1801)	Nearctic
<i>flavipes</i> LeConte, 1860	
<i>substriatum</i> Reitter, 1880	
<i>ferrugineum</i> Pic, 1920	Neotropical
<i>flavosignatum</i> Zayas, 1989	Neotropical
<i>ssp bicolorum</i> Zayas, 1989	
<i>ssp funebre</i> Zayas, 1989	
<i>ssp splendidum</i> Zayas, 1989	
<i>formosanum</i> Miwa & Mitono, 1943-	SE Asia
<i>grilloi</i> Pic, 1920	Neotropical
<i>grouvellei</i> Pic, 1920	Neotropical
<i>humale</i> Achard, 1922	Neotropical
<i>inclinans</i> Kirsch, 1873	Neotropical
<i>-javanum</i> Löbl, 1990	SE Asia
<i>khasianum</i> Löbl, 1984	SE Asia
<i>-laevisternale</i> Nakane, 1956	E Palaearctic
<i>mathami</i> R. Oberthür, 1884	Neotropical
<i>-mikado</i> Achard, 1923	E Palaearctic
<i>minutum</i> Pic, 1931	Neotropical
<i>-montanum</i> Achard, 1922	SE Asia

<i>monticola</i> Miwa & Mitono, 1943	SE Asia
<i>multistriatum</i> Pic, 1954	Africa
<i>nigronotatum</i> Pic, 1931	Neotropical
<i>oberthueri</i> Pic, 1955	Neotropical
<i>palliatum</i> Erichson, 1845	Neotropical
<i>pallidum</i> Pic, 1955	Africa
<i>peruvianum</i> Pic, 1947	Neotropical
<i>piceum</i> Reitter, 1880	S Africa
<i>plagipenne</i> Achard, 1922	SE Asia
<i>punctatum</i> Pic, 1916	SE Asia
<i>pygidiale</i> Achard, 1922	Neotropical
<i>ruficolle</i> Achard, 1922	Neotropical
<i>rufohumerale</i> Pic, 1931	Neotropical
<i>rufonotatum</i> Pic, 1916	Neotropical
<i>sallei</i> Matthews, 1888	Neotropical
<i>semirufum</i> Pic, 1917	SE Asia
<i>siamense</i> Löbl, 1990	SE Asia
<i>-sibiricum</i> Solsky, 1871	E Palaearctic
<i>submetallicum</i> Reitter, 1880	? SE Asia
<i>tamil</i> Löbl, 1979	SE Asia
<i>+terminale</i> Matthews, 1888	Neotropical
<i>tenenbaumi</i> Pic, 1926	E Palaearctic
<i>testaceicorne</i> Pic, 1931	Neotropical
<i>testaceum</i> Pic, 1920	SE Asia
<i>variabile</i> Pic, 1955	Africa
var. <i>atrocinctum</i> Pic, 1955	
var. <i>diversipenne</i> Pic, 1955	
<i>variegatum</i> Achard, 1920	SE Asia
<i>-yunnanum</i> (Achard, 1920)	SE Asia

Scaphiini *Ascaphium*

<i>-apicale</i> Lewis, 1893	E Palaearctic
<i>-minor</i> Pic, 1954	SE Asia
<i>-ochripes</i> Löbl, 1992	SE Asia
<i>-sinense</i> Pic, 1954	SE Asia
<i>-sulcipenne</i> Lewis, 1893	E Palaearctic
<i>+tibiale</i> Lewis, 1893	E Palaearctic
<i>tonkinense</i> Achard, 1921	SE Asia

Episcaphium

*transferred from *Phenoscapium*

<i>-callosipenne</i> (Achard, 1922), comb.nov.*	SE Asia
<i>+saucineum</i> (Motschulsky, 1859)	SE Asia
<i>-semirufum</i> Lewis, 1893	E Palaearctic
var. <i>ruficolle</i> Lewis, 1893	
<i>-unicolor</i> Löbl, 1992	SE Asia

Scaphium

<i>+castanipes</i> Kirby, 1837	Nearctic
<i>ferrugineum</i> Reitter, 1880	? S Africa
<i>+immaculatum</i> (Olivier, 1790)	W Palaearctic
<i>rufipes</i> Reitter, 1883	
<i>-quadraticolle</i> Solsky, 1874	C Asia

Scaphidiini
Euscaphidium

-tuberosum Achard, 1922 SE Asia

Scaphidium

* = transferred from *Scaphidiolum*

** = transferred from *Hemiscaphium*

*** = transferred from *Ascaphidium*

+ = transferred from *Scaphidiopsis*

++ = transferred from *Falsoascaphidium*

+++ = transferred from *Cribroscaphium*

- abdominale* Achard, 1920 SE Asia
abyssinicum (Pic., 1954), **comb.nov.*** Africa
alpicola Blackburn, 1891 Australia
alpiculum; Löbl, 1976 (in corr. subsequent spelling)
alternans Löbl, 1978 New Guinea
amurense Solsky, 1871 E Palaearctic
ab. bodemeyeri Reitter, 1913
andrewesi Achard, 1922 SE Asia
var. femoratum Achard, 1922
angolense Pic, 1940 Africa
angustatum Pic, 1920 Madagascar
antennatum Reitter, 1880 Nearctic
anthrax Achard, 1920 SE Asia
apicicorne (Pic, 1953), **comb.nov.*** Madagascar
-arrowi Achard, 1920 SE Asia
aterrimum Reitter, 1880 SE Asia
atricolor Pic, 1915 SE Asia
atripenne Gestro, 1879 SE Asia
atripes Pic 1946 Africa
atrosuturale Pic, 1915 SE Asia
atrum Matthews, 1888 Neotropical
baconi Pic, 1915 SE Asia
var. assamense Pic, 1915
var. multimaculatum Pic, 1915
var. semifasciatum Pic, 1915
var. uniplagatum Achard, 1922
badium Heller, 1917 SE Asia
+basale Castelnau, 1940, **comb.nov.*** Madagascar
basilewskyi (Pic, 1955), **comb.nov.*** Africa
benitense (Achard, 1922), **comb.nov.*** Africa
bicinctum Achard, 1920 SE Asia
anamalaiense Löbl, 1971
nathani Löbl, 1971
bicolor Castelnau, 1840 Madagascar
var. unicolor Castelnau, 1840
bifasciatum Pic, 1915 SE Asia
bilineatithorax (Pic, 1931), **comb.nov.*** SE Asia
binhanum (Pic, 1925), **comb.nov.*** SE Asia
binigronotatum (Pic, 1931), **comb.nov.*** Africa
binominatum Achard, 1915 SE Asia
binotatum Achard 1915 SE Asia
bipunctatum Redtenbacher, 1867 Neotropical
bisbimaculatum Pic, 1917 Neotropical
biseriatum Champion, 1927 SE Asia

<i>biundulatum</i> Champion, 1927	SE Asia
<i>bolivianum</i> (Pic, 1931), comb.nov.	Neotropical
<i>borneense</i> Pic, 1915, comb.nov.**	SE Asia
<i>-brunneopictum</i> (Achard, 1922), comb.nov.**	SE Asia
<i>carinense</i> Achard, 1920	SE Asia
<i>castaneicolor</i> Csiki, 1924	SE Asia
<i>castaneum</i> Perty, 1830	Neotropical
<i>celebense</i> Pic, 1915	SE Asia
<i>cerasinum</i> R. Oberthür, 1884	Neotropical
<i>+chapuisi</i> Gestro, 1880	SE Asia
<i>cheesmanae</i> Löbl, 1975	New Guinea
<i>chinense</i> Li, 1992	SE Asia
<i>-chujoi</i> Löbl, 1967	E Palaearctic
<i>cinnamoneum</i> Champion, 1927	SE Asia
<i>clathratum</i> Achard, 1920	SE Asia
<i>coerulans</i> Löbl, 1979	New Guinea
<i>comes</i> Löbl, 1968	E Palaearctic
<i>compressum</i> Achard, 1915	SE Asia
<i>confusum</i> (Pic, 1926), comb.nov.*	SE Asia
<i>conjunctum</i> Motschulsky, 1859	SE Asia
<i>consimile</i> Achard, 1920	SE Asia
<i>consobrinum</i> Castelnau, 1840	Madagascar
<i>-coomani</i> (Pic, 1925)	SE Asia
<i>coronatum</i> Reitter, 1880	Australia
<i>cyanellum</i> R. Oberthür, 1884	SE Asia
<i>cyanipenne</i> Gestro, 1879	New Guinea
<i>decorsei</i> Achard, 1920	Madagascar
<i>delatouchei</i> Achard, 1920	SE Asia
<i>deletum</i> Heer, 1847 (fossil)	Tertiary, Oeningen
<i>discerptum</i> (Achard, 1922), comb.nov.**	SE Asia
<i>disclusum</i> (Achard, 1924), comb.nov.*	SE Asia
<i>discoideale</i> Pic, 1920	Madagascar
<i>discomaculatum</i> (Pic, 1954), comb. nov.*	Africa
<i>disconotatum</i> Pic, 1915	SE Asia
<i>distinctum</i> Achard, 1916	Australia
<i>dohertyi</i> Pic, 1915, comb.nov.**	SE Asia
<i>donckieri</i> Pic, 1917	Madagascar
<i>dureli</i> (Achard, 1922)	SE Asia
<i>egregium</i> Achard, 1922	SE Asia
<i>elisabethae</i> (Pic, 1954), comb.nov.*	Africa
<i>ellenbergeri</i> (Paulian, 1951), comb.nov.*	Africa
<i>elongatum</i> Achard, 1915	SE Asia
<i>emarginatum</i> Lewis, 1893	E Palaearctic
<i>exclamans</i> R. Oberthür, 1884	Neotropical
<i>exornatum</i> R. Oberthür, 1884	Australia
<i>australe</i> Achard, 1916	
<i>fainanense</i> Pic, 1915	SE Asia
<i>fairmairei</i> Pic, 1920	Madagascar
<i>fasciatomaculatum</i> R. Oberthür, 1884	Neotropical
<i>fasciatum</i> Castelnau, 1840	Madagascar
<i>fascipenne</i> Reitter, 1880	Neotropical
<i>feai</i> Pic, 1920	SE Asia
<i>femorale</i> Lewis, 1893	E Palaearctic
<i>flavofasciatum</i> Champion, 1913	Neotropical
<i>flavomaculatum</i> Miwa & Mitono, 1943	SE Asia

<i>formosanum</i> Pic, 1915	SE Asia
<i>fossulatum</i> Pic, 1921	SE Asia
<i>fraternum</i> Achard, 1920	SE Asia
<i>fryi</i> Achard, 1920	SE Asia
<i>fukienense</i> Pic, 1954	SE Asia
<i>gabonicum</i> (Paulian, 1951), comb.nov.*	Africa
<i>geniculatum</i> R. Oberthür, 1884	Neotropical
<i>gestroi</i> Pic, 1920	SE Asia
<i>gibbosum</i> Pic, 1915	SE Asia
<i>gounellei</i> Pic, 1920	Neotropical
<i>gracile</i> Achard, 1920	SE Asia
<i>-grande</i> Gestro, 1880	SE Asia
<i>inimpressum</i> Pic, 1920	
<i>subannulatum</i> Pic, 1915	
var. <i>melanopus</i> Achard, 1924	
<i>grandidieri</i> Achard, 1920	Madagascar
<i>grouvellei</i> Achard, 1920	SE Asia
<i>gurung</i> Löbl, 1992	SE Asia
<i>hageni</i> Weyenbergh (fossil)	Jurassic, Solenhofen
<i>harmandi</i> Achard, 1920	SE Asia
<i>-hexaspilotum</i> (Achard, 1924)	SE Asia
<i>holzschuhi</i> Löbl, 1992	SE Asia
<i>ifanense</i> (Pic, 1947), comb.nov.*	Africa
<i>impictum</i> Boheman, 1851	S Africa
<i>impuncticolle</i> Pic, 1915, comb.nov.**	SE Asia
<i>incisum</i> Lewis, 1893	E Palaearctic
<i>incrassatum</i> Achard, 1920	SE Asia
<i>indicum</i> Löbl, 1979	SE Asia
<i>innotatum</i> (Pic, 1940), comb.nov.*	SE Asia
<i>inornatum</i> Gestro, 1880	SE Asia
<i>interruptum</i> Fairmaire, 1897	Madagascar
<i>irregularis</i> Pic, 1920, comb.nov.+++	SE Asia
<i>-jacobsoni</i> Achard, 1921	SE Asia
<i>japonum</i> Reitter, 1877	E Palaearctic
<i>japonicum</i> ; Lewis, 1893 (incorr. subsequent spelling)	
<i>longipes</i> Lewis, 1891	
<i>javanum</i> Pic, 1915	SE Asia
<i>klapperichi</i> Pic, 1954	SE Asia
<i>lafertei</i> Pic, 1920	Madagascar
<i>laosense</i> (Pic, 1928), comb.nov.*	SE Asia
<i>lateflavum</i> (Pic, 1928), comb.nov.*	SE Asia
<i>latissimum</i> Achard, 1915	Madagascar
<i>leleupi</i> (Pic, 1954), comb.nov.*	Africa
var. <i>atropygum</i> Pic, 1954	
<i>lesnei</i> Achard, 1920	SE Asia
<i>lewisi</i> (Achard, 1923), comb.nov.*	E Palaearctic
<i>lineaticolle</i> Matthews, 1888	Neotropical
<i>lineatipes</i> (Pic, 1925), comb.nov.*	Africa
<i>longicolle</i> Pic, 1915	SE Asia
var. <i>bicoloripes</i> Pic, 1948	
var. <i>kudatense</i> Pic, 1948	
<i>longipenne</i> Achard, 1921	SE Asia
<i>longithorax</i> Pic, 1916	SE Asia
var. <i>nigriventris</i> Achard, 1924	
<i>lucidum</i> Achard, 1915	Neotropical

<i>lunatum</i> Motschulsky, 1859	SE Asia
<i>lunulatum</i> ; Pic, 1921 (incorr.subsequent spelling)	
var. <i>bioculatum</i> Achard, 1924	
var. <i>inconjunctum</i> Pic, 1921	
var. <i>rufithorax</i> Pic, 1921	
<i>luteomaculatum</i> (Pic, 1923), comb.nov.*	SE Asia
<i>luzonicum</i> (Achard, 1924), comb.nov.*	SE Asia
<i>maculiceps</i> (Pic, 1923), comb.nov.*	SE Asia
<i>madecassum</i> Pic, 1917	Madagascar
<i>madurense</i> Achard, 1915	SE Asia
<i>malaccanum</i> Pic, 1915	SE Asia
<i>mangenoti</i> (Paulian, 1951), comb.nov.*	Africa
<i>marginale</i> Reitter 1880	SE Asia
<i>marginatum</i> Matthews, 1888	Neotropical
<i>martapuranum</i> Pic, 1916	SE Asia
<i>mastersi</i> Macleay, 1871	Australia
<i>matthewsi</i> Csiki, 1904	Neotropical
<i>maynei</i> (Pic, 1954), comb.nov.*	Africa
<i>medionigrum</i> Pic, 1915	SE Asia
<i>melanogaster</i> Löbl, 1992	SE Asia
<i>melli</i> Löbl, 1972	SE Asia
<i>metallescens</i> Gestro, 1879	New Guinea
<i>mexicanum</i> Castelnau, 1840	Neotropical
<i>minutum</i> Pic, 1920	SE Asia
<i>monteithi</i> Löbl, 1976	Australia
<i>montivagum</i> Shirôzu & Morimoto, 1963	E Palaearctic
<i>morimotoi</i> Löbl, 1982	E Palaearctic
<i>takashii</i> Shirôzu & Morimoto, 1963	
<i>multinotatum</i> Pic, 1921	SE Asia
<i>multipunctatum</i> (Pic, 1928), comb.nov.*	Africa
var. <i>luluanum</i> Pic, 1954	
<i>negrito</i> Heller, 1917	SE Asia
<i>nepalense</i> Löbl, 1992	SE Asia
<i>nigripes</i> Chevrolat, 1830	Neotropical
<i>nigrocinctulum</i> R. Oberthür, 1884	SE Asia
<i>nigromaculatum</i> Reitter, 1880	SE Asia
var. <i>effigiatum</i> Achard, 1922	
<i>nigrosuturale</i> Pic, 1920	SE Asia
<i>nigrum</i> Castelnau, 1840	Madagascar
<i>notaticolle</i> Pic, 1915	SE Asia
<i>notatum</i> (Pic, 1923)	Australia
<i>ocellatum</i> Achard, 1920	SE Asia
var. <i>birmanica</i> [sic] Achard, 1920	
<i>oculare</i> (Pic, 1923), comb.nov.*	Madagascar
<i>optabile</i> (Lewis, 1893)	E Palaearctic
<i>orbiculosum</i> Reitter, 1880	SE Asia
<i>ornatum</i> Casey, 1900	Nearctic
<i>overlaeti</i> (Pic, 1954), comb.nov.*	Africa
<i>palonense</i> Achard, 1920	SE Asia
<i>pantherinum</i> R. Oberthür, 1883	Neotropical
<i>papuanum</i> Löbl, 1975	New Guinea
<i>+pardale</i> Castelnau, 1840	Neotropical
var. <i>nigripenne</i> R. Oberthür, 1884	
<i>patinoi</i> R. Oberthür, 1884	Neotropical
<i>pauliani</i> nom. nov. for <i>sulcatum</i> Paulian, 1941 (secondary junior homonym of <i>S. sulcatum</i> (Pic, 1915))	Africa

<i>peninsulare</i> Achard, 1920, comb.nov.**	SE Asia
<i>peraffine</i> R. Oberthür, 1884	Neotropical
<i>-perpulchrum</i> Csiki, 1909	SE Asia
<i>philippense</i> Reitter, 1880	SE Asia
<i>phungi</i> Pic, 1923	SE Asia
<i>picconii</i> Gestro, 1880	SE Asia
var. <i>sexmaculatum</i> Reitter, 1889	
<i>piceoapicale</i> (Pic, 1940), comb.nov.*	SE Asia
<i>plagatum</i> Achard, 1920	SE Asia
<i>politum</i> Fairmaire, 1899	Madagascar
<i>prolongatum</i> (Pic, 1928), comb.nov.*	Africa
<i>pulchellum</i> Reitter, 1880	Madagascar
<i>punctaticolle</i> Pic, 1923	SE Asia
<i>punctatum</i> Castelnau, 1840	Madagascar
<i>punctipenne</i> Macleay, 1871	Australia
<i>coronatum</i> Reitter, 1880	
<i>thoracicum</i> Achard, 1916	
<i>pygidiale</i> Pic, 1917	Madagascar
var. <i>bicoloricollis</i> Pic, 1917	
+ <i>quadrigitatum</i> Say, 1823	Nearctic
<i>amplum</i> Casey, 1900	
<i>piceum</i> Melsheimer, 1846	
<i>obliteratum</i> LeConte, 1860	
<i>quadrinotatum</i> Castelnau, 1840	
<i>quadripustulatum</i> Say, 1823	
<i>quadrillum</i> Fairmaire, 1898	Madagascar
var. <i>biconjunctum</i> Pic, 1920	
<i>-quadrinotatum</i> Olivier, 1790	W Palaearctic
<i>quadrilugatum</i> Achard, 1915	SE Asia
<i>quadrilugatum</i> ; Pic, 1916 (incorr.subsequent spelling)	
<i>quadripustulatum</i> (Fabricius, 1775)	Australia
<i>bimaculatum</i> Macleay, 1871	
<i>quinguemaculatum</i> Pic, 1915	Neotropical
<i>reductum</i> (Pic, 1954), comb.nov.*	Africa
<i>reitteri</i> Lewis, 1879	E Palaearctic
<i>insulare</i> Achard, 1922	
<i>rosenbergi</i> Pic, 1955	Neotropical
<i>rouyeri</i> Pic, 1915	SE Asia
<i>rubicundum</i> Reitter, 1879	Neotropical
<i>rubricollis</i> (Pic, 1951), comb.nov.*	Madagascar
<i>rubritarse</i> Pic, 1915	SE Asia
<i>ruficolor</i> Pic, 1915	SE Asia
<i>ruficornis</i> Fairmaire, 1898	Madagascar
<i>rufipenne</i> Pic, 1917	Madagascar
<i>rufipes</i> Pic, 1922	SE Asia
<i>rufitarse</i> Achard, 1920	SE Asia
var. <i>modigliani</i> Pic, 1920	
<i>rufofemoratum</i> Pic, 1921	SE Asia
<i>rufonotatum</i> (Pic, 1928), comb.nov.*	SE Asia
<i>rufopygum</i> Lewis, 1893	E Palaearctic
<i>rufum</i> Brancsik, 1893	Madagascar
<i>-rugatum</i> Löbl, 1976	New Guinea
<i>salvazai</i> (Pic, 1928), comb.nov.*	SE Asia
<i>sauteri</i> Miwa & Mitono 1943	SE Asia
<i>semiflavum</i> Gestro, 1880	SE Asia

<i>semilimbatum</i> Pic, 1917	SE Asia
<i>septemmaculatum</i> (Pic, 1940), comb.nov.*	SE Asia
<i>septemnotatum</i> Champion, 1927	SE Asia
<i>seriatum</i> Heller, 1917	SE Asia
<i>shelfordi</i> (Achard, 1922), comb.nov.**	SE Asia
<i>shirakii</i> Miwa & Mitono, 1943	SE Asia
<i>shibatai</i> Kimura, 1987	SE Asia
<i>+sikorai</i> (Pic, 1915), comb.nov.***	Madagascar
<i>simile</i> Castelnau, 1840	Madagascar
<i>simplicicolle</i> (Pic, 1923), comb.nov.**	SE Asia
<i>sinense</i> Pic, 1954	SE Asia
<i>sinuatum</i> Csiki, 1924	SE Asia
<i>sondaicum</i> Gestro, 1880	SE Asia
<i>striatipenne</i> Gestro, 1880, comb.nov.**	SE Asia
<i>striatum</i> Pic, 1920	SE Asia
<i>suarezicum</i> Pic, 1920	Madagascar
<i>subdepressum</i> Pic, 1921, comb.nov.++	SE Asia
<i>subelongatum</i> Pic, 1915	SE Asia
<i>subpunctatum</i> (Pic, 1951), comb.nov.*	Madagascar
<i>sulcaticolle</i> (Pic, 1923), comb.nov.**	SE Asia
<i>sulcatum</i> (Pic, 1915), comb.nov.**	SE Asia
<i>sulcipenne</i> Gestro, 1880, comb.nov.**	SE Asia
<i>sylhetense</i> Achard, 1920	SE Asia
<i>takahashii</i> Miwa & Mitono, 1943	SE Asia
<i>takemurai</i> Nakane, 1956	E Palaearctic
<i>testaceum</i> Reitter, 1880	Neotropical
<i>thakali</i> Löbl, 1992	SE Asia
<i>thomasi</i> (Pic, 1926), comb.nov.*	SE Asia
<i>transversale</i> Matthews, 1888	Neotropical
<i>tricolor</i> Achard 1920, comb.nov.**	SE Asia
<i>trimaculatum</i> Löbl, 1976	Australia
<i>trinotatum</i> Pic, 1920	SE Asia
<i>tsushimense</i> Shirôzu & Morimoto, 1963	E Palaearctic
<i>tuberculipes</i> (Löbl, 1972), comb.nov.*	SE Asia
<i>undulatum</i> Pic, 1915	Neotropical
<i>unifasciatum</i> Pic, 1916	SE Asia
<i>vagefasciatum</i> Pic, 1920	Madagascar
<i>variabile</i> Matthews, 1888	Neotropical
<i>variegatum</i> Pic, 1915	Neotropical
var. <i>portevini</i> Pic, 1920	
<i>vernicaum</i> (Pic, 1954)	SE Asia
<i>vicinum</i> Pic, 1915	SE Asia
<i>violaceipenne</i> Pic, 1927	SE Asia
<i>viride</i> Löbl, 1978	New Guinea
<i>vitalisi</i> Achard, 1920	SE Asia
<i>vittipenne</i> R. Oberthür, 1884	Neotropical
<i>waterstradii</i> Pic, 1915	SE Asia
<i>yasumatsui</i> Shirôzu & Morimoto, 1963	E Palaearctic
<i>yunnanum</i> Fairmaire, 1886	SE Asia
<i>Cerambyciscapha</i>	
<i>-dohertyi</i> Pic, 1915	SE Asia
<i>Diatelium</i>	
<i>+wallacei</i> Pascoe, 1863	SE Asia
<i>spectrum</i> (Vollenhoven, 1865)	
var. <i>laterale</i> Achard, 1920	

Evolution of the *Chorthippus biguttulus* group (Orthoptera, Acrididae) in the Alps, based on morphology and stridulation

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Evolution of the *Chorthippus biguttulus* group (Orthoptera, Acrididae) in the Alps, based on morphology and stridulation. - Males of *Chorthippus biguttulus* (LINNÉ, 1758), *C. brunneus* (THUNBERG, 1815), *C. mollis* (CHARPENTIER, 1825), *C. mollis ignifer* (RAMME, 1923), *C. eisenrauti* (RAMME, 1931) and an aberrant form of *C. brunneus* (*Ticino-brunneus*) are compared on the base of morphological and acoustical characters. Discriminating morphological characters are the width of the costal and subcostal fields, the index "costal: subcostal field", the index "combined width of costal and subcostal fields: tegmen length", the index "tegmen length: length of apical area", the index "tegmen length: postfemur length", and the number of stridulatory pegs. But even in a two-character analysis there is a gradual cline of characters from *C. brunneus* via *Ticino-brunneus* and *C. eisenrauti* to *C. biguttulus*. Moreover, the range of morphological characters of *C. m. ignifer* greatly overlaps with those of *C. eisenrauti*, *Ticino-brunneus* and *C. m. mollis*. With regard to spontaneous stridulation of the males, *C. eisenrauti* differs from *C. biguttulus* in having shorter verses which are more numerous per song and in a more irregular number of syllables per echeme, of which there are usually three in *C. biguttulus*. *Ticino-brunneus* differs from nominate *C. brunneus* in producing longer verses with a higher number of pulses. The range of the verse length of *Ticino-brunneus* also overlaps with that of *C. eisenrauti*. Stridulation of *C. m. mollis* has a soft ending as in the last echemes the tick-sound is absent; in *C. m. ignifer* the song ends abruptly with a tick in the last echeme, and some echemes with a different syllable pattern can be loosely added. *C. m. ignifer* is reestablished as a good subspecies on the basis of song characters. *C. eisenrauti* is regarded to be a sister species of *C. biguttulus* conserving many of the primitive characters of the *C. biguttulus* group. A zone of transient characters between *C. eisenrauti* and *C. biguttulus* exists between Bivio and Calanda (Grisons); and a transient zone between *C. eisenrauti* and *C. brunneus* between Bregaglia and the Upper Engadine. *Ticino-brunneus* possibly evolved by hybri-

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disation between *C. eisentrauti* and *C. brunneus*. A hypothetical scheme of the evolution of the taxa of the *C. biguttulus* group occurring in the Alps is presented and discussed.

Key-words: *Chorthippus biguttulus* group - morphology - stridulation - evolution.

INTRODUCTION

Grasshoppers of the *C. biguttulus* group consist of closely related species which are difficult to separate on a morphological basis alone. They were thus for a long time mixed under the name *C. variabilis* (FIEBER, 1852) which was in use as late as FRUHSTORFER (1921) or HOFMÄNNER (1951). RAMME (1920) recognised the value of the specific stridulation for the identification of the species and proved the validity of the three "classical" species *C. biguttulus* (LINNÉ, 1758), *C. brunneus* (THUNBERG, 1815) and *C. mollis* (CHARPENTIER, 1825). Those three species were then thought to be widespread over Europe. However more recent investigations showed that their distribution is restricted to a more northerly and temperate climate and that they are replaced in southern Europe by similar, sibling species (RAGGE 1987, RAGGE *et al.* 1990, SCHMIDT 1990, BUKHVALOVA 1993). In southern Europe the full number of taxa is not yet fully known (RAGGE *et al.* 1990).

The ease with which hybrids between the different taxa are produced in the laboratory (PERDECK 1957, HELVERSEN & HELVERSEN 1975, SYCHEV 1979) shows that the *C. biguttulus* group is an assemblage of phylogenetically young species in which speciation is still in progress. Laboratory hybrids have so far been produced between *C. biguttulus* and *C. brunneus* (PERDECK 1957) as well as between *C. biguttulus* and *C. mollis* (HELVENSEN & HELVERSEN 1975, SYCHEV 1979). They were said to be fertile. Laboratory hybridisation was also possible between the Apennine form *C. rubratibialis* SCHMIDT, 1978 and *C. biguttulus*, which are said, however, to be not fully viable (SCHMIDT 1978, 1990).

In contrast to the ease with which hybrids are produced in laboratory, they are scarcely found in the field. The few specimens recorded concern hybrids between *C. brunneus* and *C. biguttulus* (KLINGSTEDT 1939, FABER 1957, PERDECK 1957, RAGGE 1976). Those findings reveal that the isolating mechanisms do work successfully in the field.

Within the region of the Alps, the three classical species and two more taxa, *C. eisentrauti* (RAMME, 1931) and *C. mollis* ignifer (RAMME, 1923) have so far been recorded (HÖLZEL 1955, SCHMIDT & BÜHL 1970, RAGGE *et al.* 1990, NADIG 1991, NADIG & THORENS 1991). However there is a great deal of controversy about the taxonomic status of the two latter and about their distribution. Moreover, there are populations with intermediate characters (NADIG & STEINMANN 1972), and an unnamed variant of *C. brunneus* has been found in the course of the present study.

C. eisentrauti was described at species level by RAMME (1931), differing slightly in both morphology and stridulation from *C. biguttulus*. However, PERDECK

(1957) considers it to be no more than a form of *C. biguttulus*. HARZ (1975) gives it specific status but suggests that it might be identical with *C. biguttulus hedickei* (RAMME, 1942). *C. b. hedickei* was described to occur from Hungary to Macedonia with the type locality Budapest, Hungary (RAMME 1951). Recent investigations on stridulation proved that the Hungarian populations belong to nominate *C. biguttulus*, and only populations from the southern Balkan differ enough to warrant subspecific status (HELVERSEN 1989, SCHMIDT 1990). The latter have been described as *C. b. euhedickei* HELVERSEN, 1989. The status of *C. eisentrauti* was reduced to subspecific level under *C. biguttulus* by SCHMIDT (1978).

C. mollis ignifer Ramme 1923 was described from South Tyrol, based on larger size and on the red colour of abdomen and hind tibiae. HARZ (1975) placed it under the synonymy of *C. mollis mollis*. But RAGGE (1981, 1984, 1987) recognised differences in the song pattern between an "alpine *mollis*" from the French Alps and nominate *C. mollis*.

The aim of the present paper focuses on two major points: (1) the taxonomic status of the different forms of the *C. biguttulus*-group as found in the Alps, and (2) the phylogenetic relations between the taxa in question.

For this purpose, a comprehensive analysis of both morphology and stridulation of numerous populations from different regions of the Alps has been done to evaluate intrapopulation as well as intra- and interspecific variation of the differential characters. The analysis concentrates on the doubtful taxa, *C. eisentrauti*, *C. mollis ignifer* and an aberrant form of *C. brunneus* referred to with the informal name "Ticino-brunneus". *C. rubratibialis* from the Apennines was included in part of the analyses. It was described as a subspecies of *C. biguttulus*, but raised to specific level by SCHMIDT (1989). Although it does not occur in the area covered by the present study, its knowledge is helpful for the understanding of the evolution of the *C. biguttulus* group. The analysis is restricted to males, as, in the *C. biguttulus*-group, the differential characters are more distinctive than in females (SYCHEV 1987).

MATERIAL AND METHODS

AREA OF RESEARCH AND ORIGIN OF SPECIMENS

Grasshopper collecting and song recording were done in the Alps and the surrounding areas in a region from the Swiss Jura, Valais and Aosta valley in the West to Carinthia and Trieste in the East (fig. 1). However, the main point of interest was on regions with populations of doubtful systematic affinities: the Insubric Region and parts of Grisons from the Upper Rhine valley to the Upper Engadine and Bregaglia. A few populations from northern Switzerland, southern Germany and the Apennines in Italy were also included. The exact localities (names in local language) are listed below. The number of recordings that were analysed is also given.

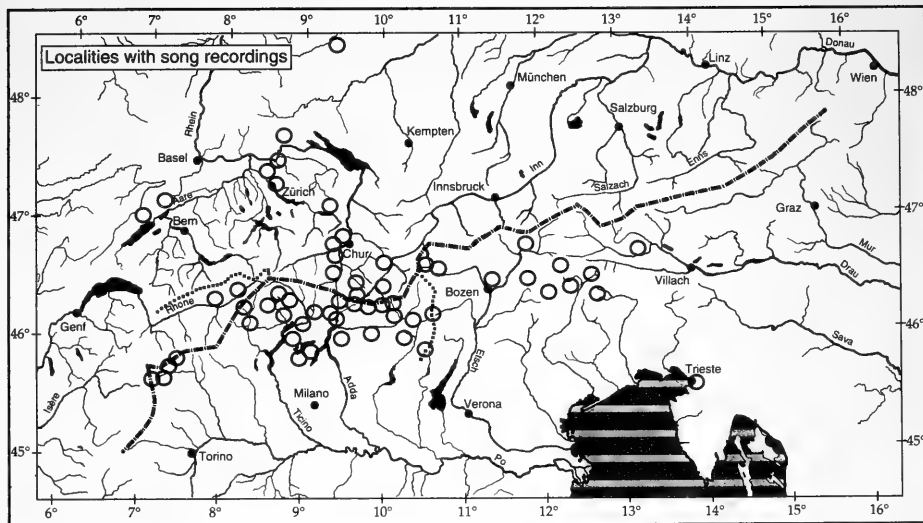


FIG. 1

Map of the area investigated. The main ridge of the Alps is indicated by the stroke-dotted line; the main ridge of Berner Alps and Adamello Alps is indicated by dotted lines. Open circles = localities with song recordings.

Chorthippus biguttulus (LINNÉ, 1758)

Switzerland: Randen (SH), Merishausen, 10.IX.1990 (3 ♂, 4 recordings); Jura (BE), Sonzeboz, 24.VIII.1991 (3 ♂, 3 recordings); Zürich (ZH), Hönggerberg, 28.X.1992 (1 ♂); Wallis, Hohtenn - Ladu, 11-1500m, 20.VII.1991 (3 ♂, 5 recordings); Churfürsten (SG), Schrina - Hochrugg, 13-1500m, 7.IX.1991 (9 ♂, 3 recordings); Churfürsten, Tschingel, 1450m, 19.VIII.1990 (6 ♂); Walenstadt, 550m, 7.IX.1991 (3 ♂, 3 recordings); Vorderrheintal (GR), Trin, 800m, 8.IX.1991 (3 ♂, 3 recordings); Hinterrheintal (GR), Reichenau, 8.IX.1991 (1 ♂); Hinterrheintal, Clugin, 1000m, 16.X.1992 (10 ♂, 38 recordings); Calanda (GR), Haldenstein, 8.X.1992 (17 ♂, 62 recordings); Calanda, Felsberg, 8.X.1992 (7 ♂, 43 recordings); Engadin (GR), Lavin, 14-1500m, 23.IX.1990 (3 ♂, 2 recordings); Val Mustair (GR), St.Maria, 13-1500m, 23.IX.1990 (4 ♂, 4 recordings). - **Italy:** Südtirol, Pustertal, Terento, 25.VII.1991 (5 ♂, 7 recordings); Grödnertal, Plan/Wolkenstein, 21.VIII.1992 (7 ♂, 19 recordings); Veneto, Belluno, Alledige - Caprile, 21.VIII.1992 (6 ♂, 21 recordings); Goima/Chiesa, 14-1500m, 23.VIII.1992 (8 ♂, 39 recordings); Forcella Lavardet, 1500m, 14.IX.1992 (5 ♂, 21 recordings); Udine, Forni di Sotto, 800m, 25.VII.1991 (3 ♂, 4 recordings). - **Austria:** Hermagor (Kärnten), Pressegger See, 600m, 16.VIII.1989 + 13.IX.1992 (5 ♂, 11 recordings).

Chorthippus eisentrauti (RAMME, 1931)

Austria: Kärnten, Hermagor, VIII.1926, lg. Eisentraut S.G., (1 ♂, Type I, Museum Berlin); Hermagor, Pressegger See, Seeblickfelsen - Rote Wand, 800-1500m, 13.IX.1992 (15 ♂, 98 recordings). - **Italy:** Südtirol, Carbonin (Schludersbach), 15-1700m, 22.VIII.1992 (10 ♂, 53 recordings); Lombardia, Brescia, Pso. di Croce Domini, 1800m, 15.VIII.1992 (6 ♂, 19 recordings); Bergamo, Pso. di Vivione, 17-1800m, 15.VIII.1992 (11 ♂, 47 recordings); Sondrio, Val Corta south of Tartano, 12-1500m, 1.IX.1991 (13 ♂, 11 recordings); Val S. Giacomo,

Fraciscio, 1450m, 15.X.1992 (19 ♂, 70 recordings); Como, Mt. Legnoncino, 15-1700m, 31.VIII.1991 (17 ♂, 16 recordings); Valle d'Aosta, Valpelline, la Lechère, 2000m, 2.IX.1991 (21 ♂ [10 ♂ ex ovo], 9 recordings); Mt. Chétif, Pra Neiron, 1800m, 3.IX.1991 (33 ♂ [16 ♂ ex ovo], 27 recordings); Pt.Serrand, 1700m, 4.IX.1991 (20 ♂ [14 ♂ ex ovo], 29 recordings). - *Switzerland*: Ticino, Mt. Generoso, 13-1500m, 8.IX.1990 (29 ♂ [19 ♂ ex ovo], 18 recordings); Mt.Lema, 16-1700m, 19.IX.1992 (11 ♂, 67 recordings); Graubünden, Bivio, Capalotta, 1800m, 16.X.1992 (11 ♂, 57 recordings); Val Bregaglia, Val da Pila, 1600m, 15.X.1992 (8 ♂, 34 recordings).

Chorthippus brunneus (THUNBERG, 1815)

Switzerland: Schöfflisdorf (ZH), 25.IX.1990 (6 ♂ [4 ♂ ex ovo], 2 recordings); Hinterrhein (GR), Reichenau, 8.IX.1991 (1 ♂); Jura (BE), Biel, 24.VIII.1991 (1 ♂, 1 recording); Sonzeboz, 24.VIII.1991 (2 ♂, 1 recording); Wallis, Hohtenn, 11-1500m, 20.VII.1991 (4 ♂, 3 recordings); Betten, 15.VI.1991 (1 ♂); Lichten, 15.VI.1991 (1 ♂); Ticino, Piano di Magadino, 18.VII.1992 (3 ♂, 9 recordings); Engadin (GR), Pontresina, 19-2300m, 17.VIII.1991 (5 ♂, 4 recordings); Madulein, 16-1700m, 23.IX.1990 (2 ♂, 3 recordings); Lavin, 14-1500m, 23.IX.1990 (2 ♂, 2 recordings); Val Mustair, St. Maria, 1400m, 23.IX.1990 (1 ♂, 2 recordings). - *Italy*: Valle d'Aosta, Valpelline, Chamer, 1700m, 2.IX.1991 (9 ♂, 4 recordings); Lombardia, Domodossola, Pontetto, 18.VII.1992 (9 ♂, 19 recordings); Sondrio, Novate Mezzola - Campo, 12.VII.1992 (5 ♂, 15 recordings). - *Austria*: Kärnten, Hermagor, Pressegger See, Seeblickfelsen, 800-1500m, 13.IX.1992 (5 ♂, 14 recordings).

Aberrant form of *C. brunneus* (= *Ticino-brunneus*)

Switzerland: Ticino, Val Vegorness north of Sonogno, 9-1300m, 9.IX.1990, 20.IX.1992 (53 ♂ (37 ♂ e.o.), 26 recordings); Bosco Gurin, 15-1800m, 21.IX.1991 (13 ♂, 12 recordings); Engadin (GR), Maloja, 1850m, 22.IX.1990 (29 ♂ [18 ♂ ex ovo], 7 recordings).

Chorthippus mollis mollis (CHARPENTIER, 1825)

Germany: Tevern (NRW), 4.IX.1992 (2 ♂, 12 recordings); Weilheim/Teck (B.-W.), 9.IX.1991 (5 ♂, 7 recordings). - *Switzerland*: Eglisau (ZH), 7.IX.1992 (6 ♂, 29 recordings); Neuchâtel (NE), 480m, 7.XI.1992, lg. P.Thorens (3 ♂, 26 recordings); Calanda (GR), Felsberg, 8.X.1992 (8 ♂, 21 recordings).

Chorthippus mollis ignifer (RAMME, 1923)

Switzerland: Wallis, Simplon Gabi, 12-1600m, 21.VII.1992 (14 ♂, 7 recordings); Hohtenn, 11-1500m, 20.VII.1992 (2 ♂, 2 recordings); Ticino, Mt. Generoso, 13-1500m, 8.IX.1990 (3 ♂, 5 recordings); Mt. S.Giorgio, 1100m, 22.IX.1991 (5 ♂, 4 recordings); Valle Maggia, Maggia, 19.VII.1992 (1 ♂, 6 recordings); Val Lavizzara, Fusio, 1250m, 21.IX.1991 (5 ♂, 2 recordings); Lago del Sambuco, 19.VII.1992 (1 ♂); Val Peccia, Cortignelli - Veia (2 ♂, 1 recording); Val Mesolcina (GR), Grono/Roveredo, 9.IX.1990 (8 ♂, 2 recordings); Val Bregaglia, Soglio, 1100m, 22.IX.1990 (23 ♂, 3 recordings); Poschiavo, s. Bernina, 1800m, 22.IX.1990 (26 ♂ [11 ♂ ex ovo], 5 recordings); Brusio, 1000m, 22.IX.1990 (6 ♂); Cavajone, 1300m, 23.IX.1990 (10 ♂, 2 recordings); Val Mustair, Tschiers - Fuldera, 1700m, 23.IX.1990 (5 ♂); St. Maria, 1400m, 23.IX.1990 (11 ♂, 3 recordings). - *Italy*: Valle d'Aosta, Valpelline, Chamer, 1700m, 2.IX.1991 (9 ♂, 5 recordings); Bionaz - Oyace, 1600m, 2.IX.1991 (12 ♂, 5 recordings); Mt. Chétif, 1800m, 3.IX.1991 (5 ♂, 6 recordings); Dolonne, 3.IX.1991 (1 ♂, 1 recording); Pt.Serrand, 1700m, 4.IX.1991 (5 ♂, 5 recordings); Lombardia, Valtellina, Valle di Mello, 1100m, 30.VIII.1991 (6 ♂, 6 recordings); Chiareggio, 1600m, 16.VIII.1992 (5 ♂, 14 recordings); Val Corta + Val Tartano, 12-1500m, 1.IX.1991 (7 ♂); Mese, Pratomorello, 1100m, 15.X.1992 (13 ♂, 39 recordings); Brescia, Galleno, 15.VIII.1992 (5 ♂, 11 recordings); Passo di Tonale,

1800m, 15.VIII.1992 (6 ♂, 13 recordings); Südtirol, Schabs - Aicha (north of Brixen), 28.VII.1990, 28.VII.1991 (5 ♂, 3 recordings); Sarntal, Schloß Wangen north of Bozen, 25.VII.1991 (2 ♂, 4 recordings); Pustertal, Niederrasen, 28.VII.1990 (2 ♂); Vintschgau, Laas, 12.VII.1990 (9 ♂); Schluders, 15.VII.1990 (3 ♂, 2 recordings); Trieste, Caresana, 26.VII.1991 (4 ♂, 6 recordings).

C. rubratibialis SCHMIDT, 1978

Italy: Toscana, Firenze, Londa - Stia, P. Jaggio Londo, 9-1100m, 3.VIII.1991 (32 ♂ [20 ♂ ex ovo], 6 recordings).

ARRANGEMENT OF POPULATIONS

The populations under study have been assigned to one of six taxa based on subjective interpretation of morphology and stridulation: *C. eisentrauti*, *C. biguttulus*, *C. brunneus*, *Ticino-brunneus*, *C. mollis* and *C. m. ignifer*. The names are those used in the literature. Moreover, the Calanda population of *C. biguttulus* was treated separately with the morphological investigations, as this population differs from nominate *C. biguttulus* in this respect. No new taxonomic name is proposed for the deviating populations of *C. brunneus*, the informal name "*Ticino-brunneus*" is used instead.

For the analysis of the morphological and acoustical characters, the local populations were either treated separately, or they were lumped to regional groups as follows: *C. eisentrauti*: (1) Pressegger See, Carbonin, (2) Insubrical Region, (3) Aosta valley, (4) Bivio; *C. biguttulus*: (5) Calanda, (6) Swiss midlands, Valais, Engadine, (7) South Tyrol, Veneto, Carinthia; *C. brunneus*: (8) *Ticino-brunneus* from Sonogno, Bosco-Gurin, (9) Maloja, (10) Insubrical Region, Aosta valley, (11) typical form from Swiss midlands, Valais, Engadine, Carinthia; (12) *C. m. mollis* from all localities north of the Alps; (13) *C. m. ignifer* from Valais and all localities on the southern side of the Alps. As the variation of morphological and behavioural characters was highest between populations within the *C. biguttulus-eisentrauti*-complex, those populations are often treated separately, while the remaining are more often lumped to regional populations.

MORPHOLOGICAL INVESTIGATIONS

Grasshoppers were collected during 2 - 4 days excursions throughout the summers of 1990 - 1992. They were brought back alive into laboratory. Of some populations, a larger series of specimens was obtained by breeding from the egg. After recording of songs and eventually oviposition, they were set as museum specimens using the freeze-drying technique. Thus no shrinking occurred during preparation. The measurement given are the same as with alive specimens.

Morphological studies and measurements were done with a WILD M5 stereo microscope using an ocular micrometer; for drawings a camera lucida was used with the same stereo microscope. Measurements and indices taken were those normally used

for separating species of the genus *Chorthippus* (HARZ 1975, RAGGE & REYNOLDS 1988) together with some additional indices which seemed promising for separating the alpine populations. Only males were studied, as they provide better diagnostic characters than the females, which are more uniform between the taxa. The following measurements or counts were taken:

- length of tegmen from base to apex;
- greatest width of tegmen (only in some of the specimens set with the wings spread away from the body);
- length of apical area from the point where the subcosta meets the costa to the tip of tegmen;
- distance from mid of stigma (a spot of white veinlets) to tip of tegmen;
- greatest width of costal field (names of veins and fields are used as in RAGGE 1955);
- width of costal and subcostal field at the greatest width of the costal field (The width of the subcostal field was then calculated by subtracting the width of the costal field from this value. The way in which the subcostal field is widened from the base to the end varies between taxa. The greatest width at the end of the subcostal field however is almost the same in all taxa except typical *C. brunneus*. Measuring the greatest width of the subcostal field is thus not very valuable);
- length of pronotum along the medial carina;
- length of prozona along the medial carina from the front margin to the principal sulcus;
- length of postfemur;
- number of stridulatory pegs on the inner side of the postfemur.

From those measurements, the following indices were calculated:

- length of tegmen: length of apical area;
- length of tegmen: distance stigma to apex of tegmen;
- length of tegmen: width of tegmen;
- width of costal: width of subcostal field;
- width of costal field: length of tegmen;
- width of costal and subcostal field: length of tegmen;
- length of prozona: length of pronotum (as a measure for the position of the principle sulcus);
- length of tegmen: length of postfemur;
- length of pronotum: length of postfemur.

No statistical tests for significance of differences in means and variance were done, as the question was not if the populations under study differ significantly in the means of their characters, which they often do between populations of the same taxon

as well, but if the differences observed and measured are relevant for the isolation between and the discrimination of the taxa.

STRIDULATION

Recordings were done in the field whenever possible. However, weather conditions and time limitations caused a high percentage of recordings to be done in the laboratory. In the latter case, males were kept separately in cages (40 x 25 x 20 cm) with a wooden frame and gauze walls. In the wooden back of the cage, a 60-Watt-bulb was mounted to provide a source of radiation and heat. All studio recordings were done between 23 and 26°C. However the position of the male close to or remote from the bulb resulted in deviating speeds of stridulation even in successive songs of the same male. Males were kept separately in the cages but within acoustical contact with other males in other cages, which stood at least three meters away from the cage with the male studied. Conditions during recording were thus resembling the conditions in the field. Completely isolated males often did not sing at all.

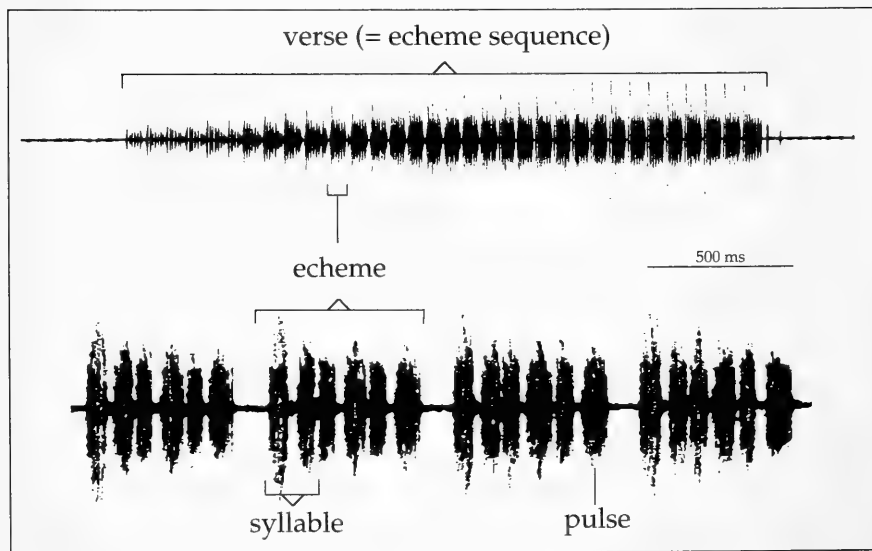


Fig. 2

Terminology of stridulation. A verse of *C. biguttulus* used as example.

Only spontaneous songs were analysed. Songs identifiable as courtship or rivalry songs were occasionally recorded but excluded from the analysis. The spontaneous song is usually heard in the field and is thus the most useful song type for identification of the species. Although analysis of courtship and rivalry songs could

be valuable for the understanding of the behaviour, including them was beyond the scope of the present work.

In *C. biguttulus* and *C. eisentrauti*, apart from normal stridulation, one-leg-songs were recorded from one or two males per population. One-leg-songs were obtained from males with one hind leg autotomised. Usually the males recovered and started to sing again within a few minutes after autotomisation. In one-leg-songs the time pattern of stridulation is more clear than in the normal two-leg-songs.

In the field, recording was done with a portable cassette recorder (Sony WM3) and a Universum microphone on CrO₂-tape cassettes; resulting frequency range 0,05 - 15 kHz. In the studio, stridulation was recorded with a cassette recorder (Kenwood KX 880 HX) and an AKG D202 microphone with the low frequency range (< 100 Hz) switched off on pure metal tape cassettes. The resulting frequency range was 0,1 - 20 kHz. In 1992, a DAT recorder (Aiwa AD-S1) together with a Sennheiser stereo microphone (MKE 66) was used instead. The frequency range was the same.

For recordings in 1990 and 1991, oscillograms were produced by an Oscillogramm (Fa. Siemens) after rerecording on an Uher Report M4200 tape recorder. For recordings in 1992, analysis of stridulation was done using the programme Sound-scope on a Macintosh PC (Quadra 800) with a MacAdios II/16 board as A/D converter which was connected via a MacAdios ABO box to the cassette or DAT recorder.

For the description of songs the following terminology is used (fig. 2): syllable, one complete down and up movement of the hind legs, echeme, first order assemblage of syllables, verse (= echeme-sequence in RAGGE & REYNOLDS 1988), first order assemblage of echemes.

One song per male was analysed of the 1990 and 1991 recordings, whereas 3 - 6 songs per male of the 1992 recordings. In order to exclude the effect of temperature on speed and duration of the stridulation, the number of syllables (*C. biguttulus* and *C. eisentrauti*), pulses (*C. brunneus*) or echemes (*C. mollis*) per larger song unit were used as the main measures for the song duration. Due to greater differences in song pattern, the analysis of the song characters was done separately for the following three groups: (1) *C. biguttulus* and *C. eisentrauti*, (2) *C. brunneus*, (3) *C. mollis* and *C. m. ignifer*.

RESULTS

MORPHOLOGY

Shape and venation of tegmen

The shape of the male tegmen and the relative widths of the costal and sub-costal fields are usually regarded as the most relevant morphological characters for identifying species of the *C. biguttulus* group (RAMME 1923, HARZ 1975, SCHMIDT

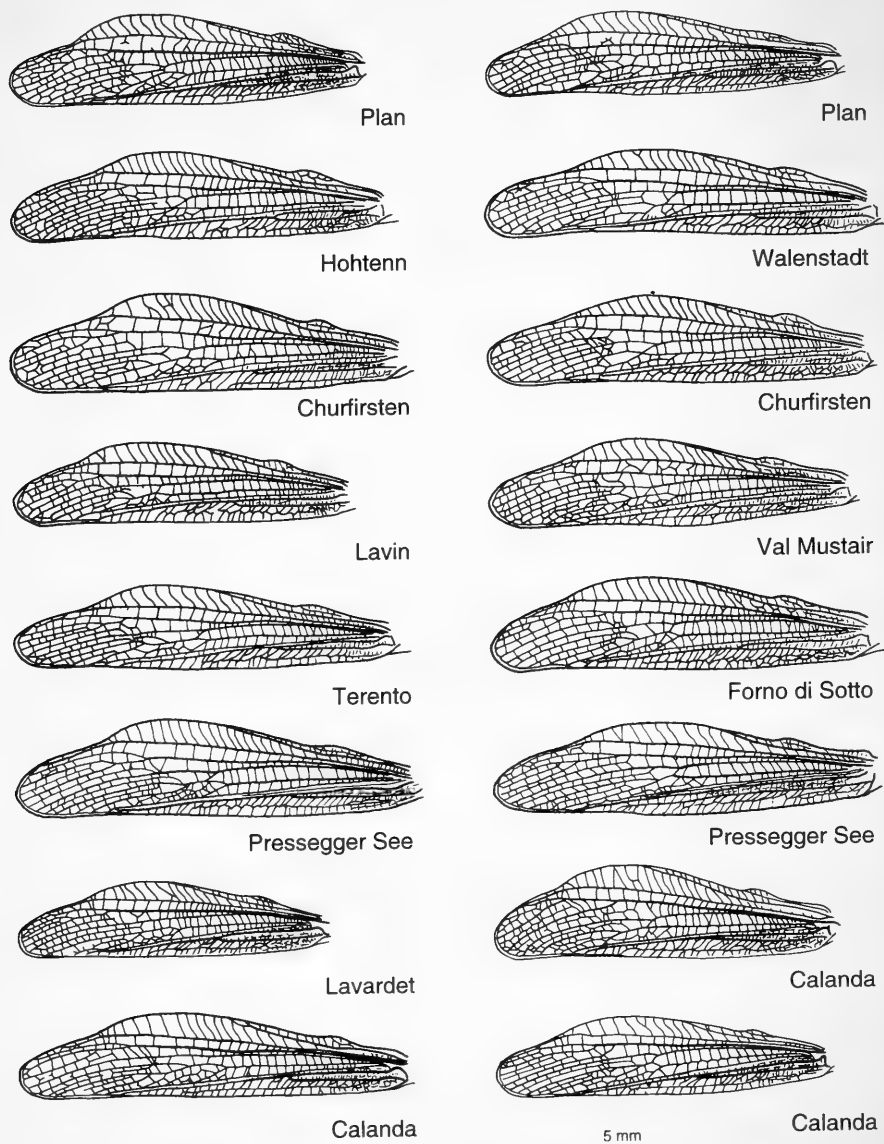
Chorthippus biguttulus

FIG. 3

Variation of the left tegmen of males of *C. biguttulus* from different populations of the Alps and the northern Prealps.

1978, SYCHEV 1987, RAGGE & REYNOLDS 1988). The variation of the tegmen between and within populations was thus studied in detail.

The tegmen of *C. biguttulus* is characterised by a distinct widening of both the costal and the subcostal fields (fig. 3). The subcostal field is suddenly widened behind the basal third of the tegmen and then remains of about equal width until the apical constriction. In about the apical quarter of the tegmen, both fields are suddenly constricted, resulting in a flexion or almost indentation at the anterior margin of the tegmen. Those characters are usually very distinct in specimens which live north of the Alps and on the southern side of the Alps in South Tyrol (fig. 3, Plan left). However they are subject to individual variation and in some specimens are less distinct (fig. 3). On the southern side of the Alps, the tegmina are slightly more slender with the widening of the costal and subcostal fields and thus the flexion less extreme. But also north of the Alps, populations with rather slender tegmina have been found. In the Calanda population, most males have tegmina with the subcostal field only weakly widened. They are thus more slender and resemble those of *C. eisenrauti*. However, males with typical *C. biguttulus* tegmina and transient forms also occur in the same population (fig. 3). Moreover, even in tegmina with a rather narrow subcostal field, the sudden widening behind the basal third of the tegmen is obvious. On the Churfürsten (including Walenstadt at the base of the Churfürsten), many males are rather large and have tegmen with a prolonged apical area and less widened costal and subcostal fields. However again, all transient forms to the typical *C. biguttulus* shape exist. In Pressegger See, the type locality of *C. eisenrauti*, nominate *C. biguttulus* were found at the base of the Seeblickfelsen. The tegmina varied between the two extremes shown in fig. 3: one has the shape typical for *C. biguttulus*, the other is rather slender, but the widening of the subcostal field is still distinct.

The tegmen of *C. eisenrauti* is similar to that of *C. biguttulus* insofar as the costal field is distinctly widened and the tegmen subapically constricted (fig. 4). The apical area is often longer than in *C. biguttulus*. The subcostal field is rather variable even within populations. Typically, it is gradually widened from the base until the subapical constriction of the tegmen. In some specimens it remains narrow until the apical constriction (but never so narrow as in nominate *C. brunneus*), while again in others there is a faint indication of a sudden widening behind the basal third of the tegmen as in *C. biguttulus*. The widening of the subcostal field is however not so strong as in the typical *C. biguttulus* tegmen. Anyhow, as the variation is great, single individuals of *C. eisenrauti* may be confused with *C. biguttulus* on the one hand or with *C. mollis ignifer* or aberrant forms of *C. brunneus* on the other.

The tegmen of *C. mollis ignifer* is almost identical with that of *C. eisenrauti*, although the apical area is usually slightly shorter, the costal field slightly less widened and the subcostal field more regularly widened from the base until the subapical constriction of the tegmen (fig. 5). As all of those characters are variable, confusion of single specimens with those of *C. eisenrauti* is possible. Often specimens of *C. mollis ignifer* are smaller than those of *C. eisenrauti*, but some populations consist of rather large individuals that may be easily confused with the latter.

Chorthippus eisentrauti

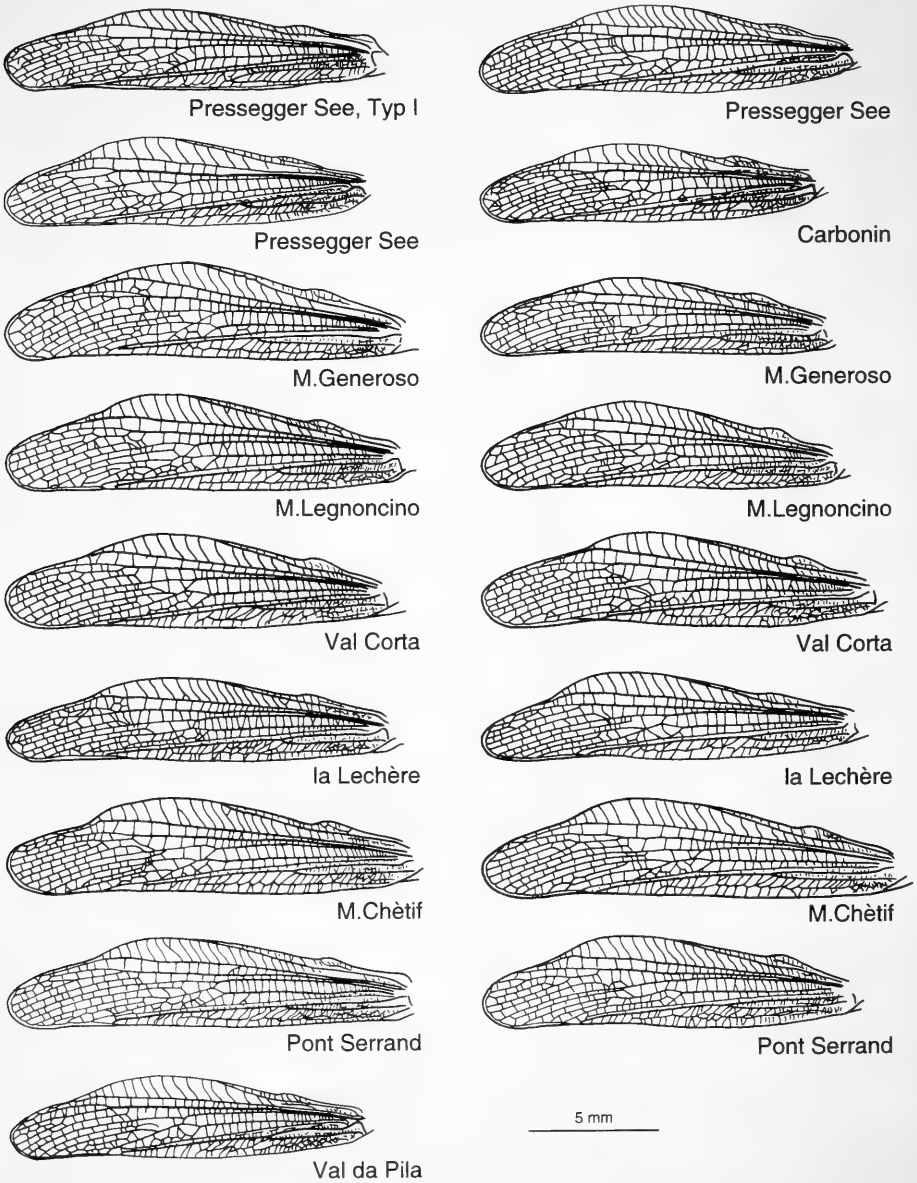


FIG. 4

Variation of the left tegmen of males of *C. eisentrauti* from different populations of the Alps.

The difference between *C. mollis mollis* and *C. mollis ignifer* lies mainly in the size of the tegmen. In the mean, the apical area is slightly shorter in *C. mollis* than in *C. m. ignifer*. However, populations from the Swiss midland consist of larger individuals than in the northern German plain (fig. 5). There is thus a great deal of overlap between those populations and *C. mollis ignifer*.

C. brunneus has the longest tegmen which is of almost equal width throughout (fig. 5). In the nominate form, the costal field is only faintly widened and the subcostal field is hardly widened or almost not widened at all; there is only a faint apical constriction, the anterior margin thus being without flexion. The apical area is long. This typical form was found north of the Alps, in Valais and in Carinthia. The tegmina of the populations from the Insubrical Region and the Engadine more or less approach the shape of *C. mollis ignifer* and *C. eisentrauti*. This is most distinct in specimens from Maloja, Sonogno and Bosco-Gurin, in which the costal field is distinctly widened, the apical area shortened and the flexion of the anterior margin of the tegmen distinct (fig. 5). Only the subcostal field is usually less widened than in *C. m. ignifer*. Specimens from the latter three populations are referred to as *Ticino-brunneus*, as stridulation also deviates from the nominate form.

Finally, the tegmen of *C. rubratibialis* from the Apennines is intermediate between *Ticino-brunneus*, *C. mollis ignifer* and *C. eisentrauti*. It has a long apical area, the costal field moderately to distinctly widened and the subcostal field moderately widened. The subapical constriction of the tegmen is present but weak (fig. 5).

The above descriptions reveal that the typical forms of the tegmen of *C. biguttulus*, *C. brunneus* and *C. mollis* are quite distinct. On the other hand, southern alpine populations of the different taxa are approached to each other. Thus a diagnosis based on morphological characters alone might prove difficult or impossible. It is thus necessary to test if morphometrical data of a single character or a combined set of several characters can help in identifying the specimens and help with the question about the validity of the taxa.

Statistical analysis of morphological characters

The ranges, means and standard deviations for all measurements and calculations of indices done are summarised for regional populations in tab. 1 and 2. Only for the more relevant characters are population means presented in graphs.

Length of tegmen

There is a tendency that populations of *C. brunneus* and *C. eisentrauti* have the longest tegmina, those of *C. mollis* the shortest. However, there is a great range of overlap (fig. 6). Moreover, populations of *C. eisentrauti* from Carbonin and from localities north of the Valtellina valley in northern Italy as well as populations of *Ticino-brunneus* and *C. brunneus* from the Engadine have tegmen not longer than average for *C. biguttulus*. Within *C. mollis*, the length of the tegmen varies more between populations than between the northern (*C. m. mollis*) and the southern form

Chorthippus brunneus



Schöfflisdorf



Hohtenn

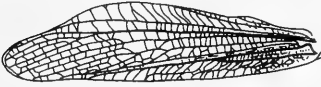


Pontresina



P.d.Magadino

Chorthippus mollis mollis



Eglisau

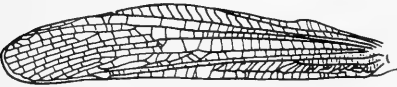


Calanda



Teverener Heide

Chorthippus rubratibialis



Londo - Stia

Ticino-brunneus



Maloja

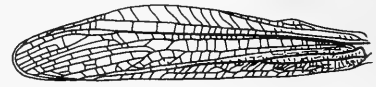


Bosco Gurin



Val Vegorress

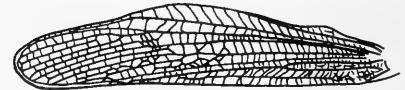
Chorthippus mollis ignifer



Sarntal



Grono

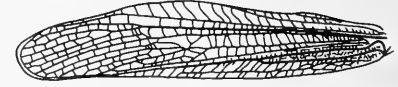


M.S. Giorgio



Chamère

5 mm



Londo - Stia

FIG. 5

Variation of the left tegmen of males of *C. brunneus* (Alps and Swiss midlands), *Ticino-brunneus* (Ticino and Maloja), *C. m. mollis* (Swiss midlands and northern Germany), *C. m. ignifer* (southern Alps) and *C. rubratibialis* (Apennines).

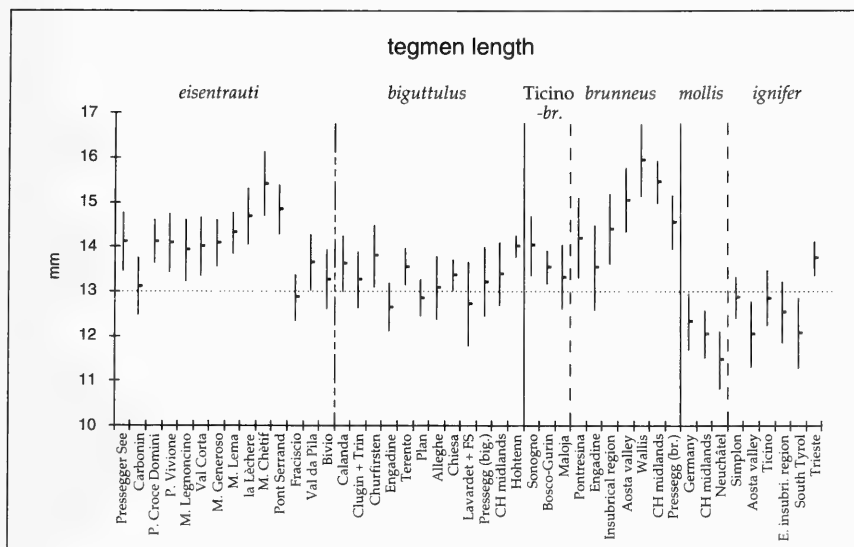


FIG. 6

Comparison of the tegmen length in populations of the *C. biguttulus* group from the Alps and surrounding regions. Means and standard deviations are given.

(*C. m. ignifer*). Although some of the southern populations have the means of the wing length as long as in *C. biguttulus*, the values for the Aosta and the South Tyrol populations are not longer than those for specimens from the Swiss midlands.

Index "tegmen : postfemur"

Differences in wing length can result from differences in overall body size or from differences in the shape of the tegmen. To exclude differences resulting from overall body size, an index "tegmen : postfemur" was calculated. This index reveals no differences between *C. eisenrauti*, *C. biguttulus*, *Ticino-brunneus* and *C. brunneus* from Engadine (fig. 7): within form variation is larger than between form variation. That means the differences in wing length between *C. eisenrauti* and *C. biguttulus* are mainly due to differences in overall body size. However in nominate *C. brunneus* (except in the Engadine populations) this index is higher. That means the wings are longer even compared with overall body size. In *C. mollis* (including *ignifer*) this index and thus the relative wing length is on average lower than in *C. biguttulus* and *C. eisenrauti*, but with the ranges largely overlapping. There are no differences between *C. mollis mollis* and *C. mollis ignifer*, although in the Neuchâtel population the mean of this index is the lowest measured. Within *C. eisenrauti*, the

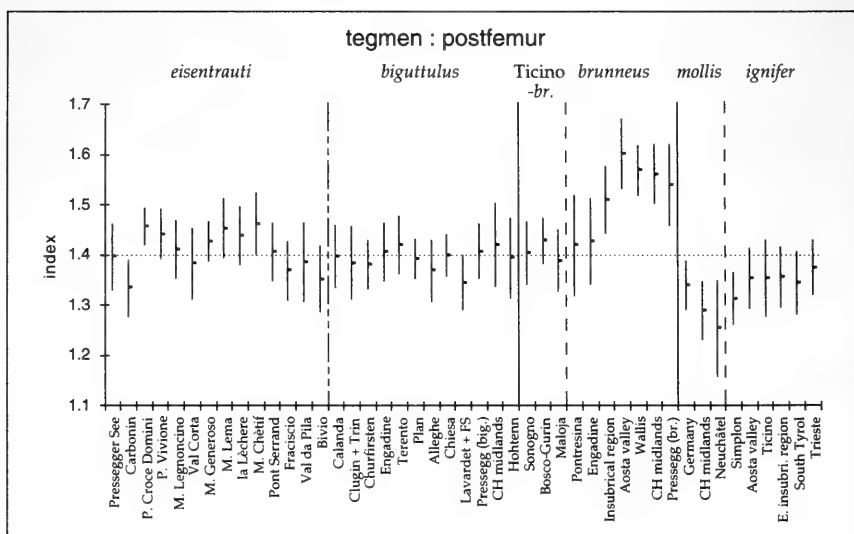


FIG. 7

Comparison of the index "tegmen length : postfemur length" in populations of the *C. biguttulus* Ogroup from the Alps and surrounding regions. Means and standard deviations are given.

populations with the shortest tegmina also have the lowest index (Carbonin and north of Valtellina valley); showing that those populations are not generally smaller but have relatively shorter wings. The relative length of the tegmen may help to identify nominate *C. brunneus* except for the Engadine populations, but not to differentiate between any other forms.

Index "tegmen length : tegmen width"

Differences in the shape of the tegmen can result from (1) differences in the length to width index or (2) from differences between the size of different areas of the tegmen. The width of the tegmen was only measured in relatively few specimens with the wings spread away from the body. In specimens with the wings along the body, its width cannot be taken with enough accuracy to be reliable in a comparative study. In the *C. biguttulus* and *C. eisentrauti* populations, the means of the index "tegmen length : tegmen width" are lower than the general mean over all taxa; in the *C. brunneus* populations they are always higher, while in the *C. mollis* populations they are scattered around the general mean. However, individual variation is high, and the ranges overlap greatly between forms. This index is thus not a valuable character for separating the different taxa (data see tab. 1 + 2).

Length of apical area of tegmen

The comparison of the tegmen (figs. 3-5) reveals that the length of the apical area of the tegmen varies between taxa: it is usually long in *C. brunneus*, short in *C. mollis* and of intermediate length in *C. biguttulus* and *C. eisentrauti*. Two measurements were taken to find out whether those differences are reliable: (1) the length of the apical area measured from the point where the subcosta meets the anterior margin of the tegmen to the tip of the tegmen, (2) the distance between the middle of the stigma to the tip of the tegmen. Their size relative to the wing length was estimated by calculating the indices "tegmen : apical area" and "tegmen : stigma". Both indices show the same differences between populations and taxa. The second index however is due to greater individual variation. Thus only the first is described in detail.

First it is striking that the index "tegmen length : apical area" separates *C. brunneus* (including the Ticino-form) from *C. biguttulus* (fig. 8). There is no or only a minor overlap of values except for the Alpe di Siusi population of *C. biguttulus*. On the other hand, this character is highly variable within *C. eisentrauti* and within *C. mollis*. In *C. eisentrauti*, specimens from the type locality (Pressegger See), the Aosta valley, Val da Pila and Bivio agree in this character with *C. biguttulus*, while those from Ticino, Val Corta, Passo Vivione, Passo di Croce Domini and Carbonin are more close to *C. brunneus*, with values almost the same as in the Ticino-form. Populations from Mt. Legnoncino and Fraciscio are in between. In *C. mollis* there are no differences between the nominate form and *C. m. ignifer*, but large differences between populations from different areas. The range of *C. mollis* overlaps with *C. biguttulus*, *C. eisentrauti* and Ticino-*brunneus*. Within *C. brunneus*, the index is higher in the Ticino-form and in the Engadine populations than in the nominate form. That means individuals of those populations have the apical area relatively short compared with the nominate form.

Width of costal and subcostal fields of tegmen

The costal and subcostal fields of the tegmen are usually widened in *C. biguttulus*, while they are comparatively narrow in *C. brunneus* (figs. 3-5). In *C. eisentrauti* and in *C. mollis* (including *ignifer*), the costal field is wide, while the subcostal field is gradually widening from base to apex. Thus its width may vary considerably in the same specimen, depending on the point of measurement. In this study, the subcostal field was always measured at the point where the costal field has its largest width. Two measurements were taken and used for comparing the species under study: the width of the costal field and the width of the costal plus subcostal fields. Both values show exactly the same variation between population and species, but the second differentiates more clearly between taxa and is thus the only one discussed below.

Considering the means and standard deviations of the measurement "width of costal plus subcostal field", the taxa can be subdivided into two groups: *C. biguttulus* and *C. eisentrauti* on the one hand and *C. brunneus* and *C. mollis* on the other (data see

TAB. 1

Morphometrical data of *Chorthippus biguttulus* and *C. eisentrauti*. Minimum, maximum, mean, standard deviation and number of observations are given. Local populations are clustered to regional groups.

	<i>eisentrauti</i>				<i>biguttulus</i>		
	Pressegger See, Carbonin	Insubrical Region	Aosta valley	Bivio	Calanda	CH midlands, Valais, Engadine	South Tyrol, Veneto, Carinthia
Tegmen length (mm)	12.2-15.4 13.76±0.79 n=23	12.1-15.1 13.84±0.72 n=108	13.7-17.4 15.06±0.72 n=72	12.1-14.1 13.27±0.65 n=11	12.2-14.7 13.62±0.62 n=23	12.2-14.9 13.49±0.73 n=44	11.6-14.3 13.09±0.65 n=42
Apical area (mm)	2.86-3.81 3.36±0.29 n=23	2.72-4.35 3.57±0.37 n=108	2.86-4.62 3.51±0.36 n=72	2.72-3.26 3.05±0.19 n=11	2.45-3.81 3.12±0.29 n=23	2.45-3.67 3.02±0.26 n=44	2.45-3.81 3.00±0.26 n=42
Stigma - apex (mm)	4.01-5.30 4.60±0.36 n=23	3.81-5.98 4.91±0.41 n=108	4.62-6.53 5.26±0.46 n=72	3.94-4.76 4.35±0.26 n=11	3.94-5.03 4.53±0.32 n=23	3.54-5.30 4.45±0.41 n=44	3.54-4.90 4.30±0.35 n=42
Tegmen width (mm)	2.92-3.47 3.15±0.18 n=9	2.72-3.60 3.23±0.18 n=40	3.13-3.54 3.32±0.14 n=11	3.13-3.40 3.28±0.10 n=5	2.99-3.40 3.17±0.16 n=10	2.92-3.60 3.21±0.19 n=15	2.86-3.47 3.24±0.16 n=16
Tegmen / apical area	3.69-4.57 4.11±0.30 n=23	3.41-5.05 3.91±0.32 n=108	3.59-5.24 4.32±0.33 n=72	4.04-4.80 4.35±0.26 n=11	3.79-5.00 4.39±0.31 n=23	3.78-5.25 4.49±0.31 n=44	3.67-5.05 4.39±0.35 n=42
Tegmen / stigma	2.62-3.23 3.00±0.18 n=23	2.50-3.27 2.83±0.15 n=108	2.59-3.20 2.88±0.16 n=72	2.77-3.35 3.05±0.18 n=11	2.78-3.21 3.01±0.13 n=23	2.68-3.56 3.05±0.20 n=44	2.66-3.63 3.06±0.20 n=42
Tegmen length / width	4.00-4.82 4.37±0.29 n=9	3.92-4.80 4.30±0.20 n=40	4.04-4.74 4.40±0.21 n=11	3.71-4.39 4.11±0.27 n=5	3.80-4.70 4.29±0.27 n=10	3.88-4.88 4.23±0.25 n=15	3.84-4.39 4.10±0.14 n=16
Costal field (mm)	0.71-0.91 0.77±0.05 n=23	0.65-0.97 0.82±0.06 n=108	0.78-1.20 0.94±0.07 n=72	0.75-0.88 0.81±0.05 n=11	0.68-0.88 0.79±0.06 n=23	0.68-0.97 0.81±0.06 n=44	0.68-0.97 0.80±0.06 n=42
Costal and subcostal fields (mm)	1.04-1.36 1.19±0.09 n=23	0.97-1.40 1.19±0.08 n=108	1.17-1.53 1.35±0.08 n=72	1.14-1.30 1.22±0.06 n=11	1.04-1.36 1.19±0.08 n=23	1.10-1.46 1.30±0.08 n=44	1.10-1.49 1.28±0.09 n=42
Costal / subcostal field	1.33-2.20 1.88±0.20 n=23	1.69-2.80 2.22±0.25 n=108	1.71-3.70 2.31±0.33 n=72	1.79-2.45 2.00±0.22 n=11	1.63-2.45 2.00±0.24 n=23	1.28-2.50 1.69±0.24 n=44	1.33-2.17 1.70±0.20 n=42
Costal+subcostal fields / tegmen	0.08-0.10 0.09±0.01 n=23	0.08-0.10 0.09±0.01 n=108	0.08-0.10 0.09±0.00 n=72	0.08-0.10 0.09±0.01 n=11	0.08-0.11 0.09±0.01 n=23	0.08-0.11 0.10±0.01 n=44	0.09-0.11 0.10±0.01 n=42
Costal field / tegmen	0.05-0.07 0.06±0.00 n=23	0.05-0.07 0.06±0.00 n=108	0.05-0.07 0.06±0.00 n=72	0.05-0.07 0.06±0.00 n=11	0.05-0.07 0.06±0.00 n=23	0.05-0.07 0.06±0.00 n=44	0.05-0.07 0.06±0.00 n=42
Pronotum (mm)	3.12-3.63 3.38±0.16 n=23	2.86-3.63 3.21±0.16 n=106	3.12-3.89 3.54±0.16 n=72	3.05-3.57 3.35±0.16 n=11	2.99-3.57 3.22±0.15 n=23	2.92-3.76 3.31±0.22 n=44	2.86-3.50 3.21±0.19 n=42
Prozona (mm)	1.49-1.78 1.61±0.08 n=23	1.30-1.69 1.47±0.08 n=106	1.36-1.82 1.62±0.08 n=72	1.36-1.65 1.54±0.08 n=11	1.36-1.62 1.48±0.07 n=23	1.30-1.78 1.52±0.11 n=44	1.30-1.65 1.46±0.09 n=42
Prozona / pronotum	0.45-0.50 0.48±0.01 n=23	0.41-0.51 0.46±0.02 n=106	0.39-0.49 0.46±0.02 n=72	0.43-0.49 0.46±0.02 n=11	0.42-0.50 0.46±0.02 n=23	0.43-0.51 0.46±0.02 n=44	0.42-0.48 0.45±0.02 n=42
Postfemur (mm)	9.11-10.88 10.01±0.40 n=23	8.57-10.88 9.80±0.42 n=108	9.52-11.70 10.46±0.47 n=72	9.11-10.34 9.82±0.35 n=11	8.84-10.74 9.76±0.52 n=23	8.43-10.47 9.71±0.56 n=44	8.30-10.61 9.42±0.43 n=42
Tegmen / postfemur	1.26-1.52 1.37±0.07 n=23	1.26-1.56 1.41±0.06 n=108	1.30-1.57 1.44±0.06 n=72	1.23-1.46 1.35±0.07 n=11	1.30-1.52 1.40±0.06 n=23	1.26-1.56 1.39±0.06 n=44	1.27-1.49 1.39±0.06 n=42
Pronotum / postfemur	0.31-0.37 0.34±0.01 n=23	0.29-0.35 0.32±0.05 n=108	0.31-0.37 0.34±0.01 n=72	0.32-0.36 0.34±0.02 n=11	0.31-0.37 0.33±0.01 n=23	0.31-0.37 0.34±0.01 n=44	0.31-0.37 0.34±0.01 n=42
Stridulatory pegs	83-127 104.7±10.7 n=22	87-139 110.2±10.5 n=108	88-135 109.3±11.0 n=32	88-124 107.1±10.5 n=11	93-131 111.6±9.0 n=23	84-126 103.5±10.4 n=25	88-138 106.2±12.4 n=28
Stridulatory pegs / postfemur	8.36-12.79 10.47±1.09 n=22	9.27-14.40 11.26±1.01 n=108	8.74-13.45 10.71±1.21 n=32	8.99-12.40 10.92±1.14 n=11	9.50-13.76 11.49±1.32 n=23	8.84-12.08 10.60±0.96 n=25	9.42-14.29 11.37±1.21 n=28

tab. 1 + 2). There is little overlap with regard to the standard deviations between both groups. Unfortunately, this character is not useful to differentiate between *C. biguttulus* and *C. eisentrauti*, nor between *C. brunneus* and *C. mollis*. Generally, the mean values are slightly higher in *C. biguttulus* than in *C. eisentrauti*, but in *C. eisentrauti* populations from the Aosta valley they are higher than in *C. biguttulus*. In *C. biguttulus* from Calanda, the width of the costal and subcostal fields are lower than usual for *C. biguttulus* and agree with *C. eisentrauti*. The Carbonin population of *C. eisentrauti* has rather narrow costal and subcostal fields and the values thus overlap largely with values for *C. mollis ignifer*. Within the second group, the mean values for nominate *C. mollis* and *C. brunneus* are lower than those of *C. m. ignifer* and Ticino-brunneus. However with a large overlap in the standard deviations.

As the width of the costal and subcostal fields relative to each other differs between taxa, the index "costal : subcostal field" promised to be a useful character for determination (fig. 9). At first glance, there is a clear difference of the mean values between the taxa: In *C. brunneus* and in most populations of *C. eisentrauti*, the costal field is more than twice as wide than the subcostal field. In *C. biguttulus* it is less than twice as wide, except in the Calanda population. Finely, in *C. mollis* (including *C. m. ignifer*), the costal field is about twice as wide as the subcostal field. However, there is a large overlap between *C. mollis* and all other forms, and between *C. eisentrauti* and both *C. brunneus* and *C. biguttulus*. This character can thus only be helpful in determination if we can compare large numbers of specimens. Moreover, there are some important exceptions in the *C. biguttulus-eisentrauti*-complex. The most relevant exception is that the value for *C. eisentrauti* from the type locality is almost the same as in nominate *C. biguttulus*. In most specimens the costal field is less than twice as wide than the subcostal field. Other more eastern (Carbonin, Croce Domini) and the northernmost populations (Bivio) of *C. eisentrauti* as well as the Calanda population of *C. biguttulus* have the costal field about twice as wide as the subcostal field. They are thus transient between *C. biguttulus* and more extreme forms of *C. eisentrauti* and agree with *C. mollis* with regard to this character.

Two indices were calculated relating the widening of the costal and/or subcostal fields to the wing length: (1) "costal field: tegmen length" and (2) "costal + subcostal fields: tegmen length". Both show the same trend, but the second differentiates better between taxa. It is thus dealt with in detail (fig. 10).

The index "costal + subcostal fields : tegmen length" is usually greater 0.08 in *C. biguttulus* and *C. eisentrauti*, lower than 0.08 in *C. brunneus* including the Ticino-form, but varying between 0.07 and 0.09 in *C. m. mollis* and *C. mollis ignifer*. The index thus differentiates between *C. biguttulus* and *C. brunneus* with only a minor overlap between Ticino-brunneus and the Calanda populations of *C. biguttulus*. But, on the other hand, it does not allow differentiation between both subspecies of *C. mollis* and either *C. eisentrauti* or Ticino-brunneus.

Using the population means, this index even allows differentiation between *C. eisentrauti* and *C. biguttulus* except for the Calanda population. The means for the former vary between 0.08 and 0.09, for the latter between 0.09 and 0.10. However overlapping is such that single individuals cannot be separated by this character alone.

TAB. 2

Morphometrical data of *Chorthippus brunneus* and *C. mollis*. Minimum, maximum, mean, standard deviation and number of observations are given.

	Ticino-brunneus		brunneus		<i>m. mollis</i>	<i>m. ignifer</i>
	Sonogno, Bosco-Gurin	Maloja	Insubrical Region, Aosta valley	CH midlands, Valais, Enga- dine, Carinthia		
Tegmen length (mm)	11.8-15.2 13.93±0.64 n=63	11.9-15.2 13.32±0.71 n=28	12.9-16.3 14.60±0.80 n=25	12.6-16.7 14.92±1.07 n=29	10.7-13.1 12.04±0.60 n=23	10.1-14.0 12.48±0.75 n=222
Apical area (mm)	2.86-4.76 3.84±0.34 n=63	3.13-3.94 3.50±0.24 n=28	3.81-5.44 4.51±0.44 n=25	3.54-5.30 4.43±0.49 n=29	2.31-3.54 2.83±0.27 n=23	2.18-4.22 3.01±0.38 n=222
Stigma - apex (mm)	3.40-5.98 5.02±0.44 n=63	4.49-5.58 4.96±0.28 n=28	4.56-6.66 5.78±0.46 n=25	4.76-6.80 5.85±0.59 n=29	3.40-5.10 4.14±0.38 n=23	2.86-5.44 4.22±0.45 n=222
Tegmen width (mm)	2.79-3.40 3.03±0.17 n=13	2.72-3.20 2.92±0.17 n=9	2.58-3.13 2.88±0.20 n=5	2.65-3.33 2.95±0.22 n=9	2.31-2.99 2.58±0.24 n=6	2.45-3.20 2.83±0.16 n=48
Tegmen / apical area	3.17-4.35 3.64±0.23 n=63	3.44-4.17 3.81±0.19 n=28	2.84-3.69 3.25±0.22 n=25	2.97-3.81 3.39±0.21 n=29	3.54-4.83 4.29±0.31 n=23	3.29-5.31 4.19±0.40 n=222
Tegmen / stigma	2.49-4.00 2.79±0.21 n=63	2.51-2.91 2.69±0.09 n=28	2.31-2.84 2.53±0.11 n=25	2.39-2.86 2.56±0.12 n=29	2.55-3.28 2.92±0.18 n=23	2.50-4.05 2.97±0.21 n=222
Tegmen length / width	3.52-5.02 4.61±0.38 n=13	4.57-5.00 4.74±0.14 n=9	4.65-5.71 5.08±0.39 n=5	4.64-5.81 5.12±0.33 n=9	3.91-4.89 4.59±0.36 n=6	3.77-4.84 4.46±0.22 n=48
Costal field (mm)	0.58-0.81 0.70±0.05 n=63	0.58-0.78 0.66±0.05 n=28	0.58-0.78 0.68±0.05 n=25	0.49-0.75 0.65±0.06 n=29	0.52-0.71 0.61±0.05 n=23	0.55-0.78 0.67±0.04 n=222
Costal and subcostal fields (mm)	0.88-1.17 1.02±0.06 n=63	0.84-1.04 0.94±0.06 n=28	0.88-1.14 0.97±0.07 n=25	0.78-1.07 0.93±0.07 n=29	0.81-1.07 0.92±0.06 n=23	0.88-1.23 1.02±0.06 n=222
Costal / subcostal field	1.82-2.88 2.27±0.25 n=63	1.90-3.00 2.34±0.34 n=28	1.90-3.00 2.35±0.29 n=25	1.67-3.00 2.34±0.30 n=29	1.78-2.50 2.04±0.18 n=23	1.38-2.88 1.95±0.21 n=222
Costal+subcostal fields / tegmen	0.06-0.09 0.07±0.01 n=63	0.06-0.08 0.07±0.00 n=28	0.06-0.07 0.07±0.00 n=25	0.05-0.07 0.06±0.00 n=29	0.07-0.09 0.08±0.01 n=23	0.07-0.11 0.08±0.01 n=222
Costal field / tegmen	0.04-0.06 0.05±0.00 n=63	0.04-0.06 0.05±0.00 n=28	0.04-0.05 0.05±0.00 n=25	0.04-0.05 0.04±0.00 n=29	0.04-0.06 0.05±0.00 n=23	0.04-0.07 0.05±0.00 n=222
Pronotum (mm)	2.73-3.57 3.12±0.15 n=63	2.66-3.37 3.07±0.14 n=28	2.63-3.31 3.05±0.18 n=25	2.79-3.44 3.19±0.15 n=29	2.63-3.25 2.95±0.16 n=23	2.60-3.44 3.03±0.16 n=222
Prozona (mm)	1.17-1.53 1.37±0.08 n=63	1.33-1.53 1.41±0.05 n=28	1.17-1.43 1.32±0.07 n=25	1.23-1.53 1.39±0.08 n=29	1.23-1.56 1.39±0.08 n=23	1.23-1.72 1.43±0.09 n=222
Prozona / pronotum	0.40-0.48 0.44±0.02 n=63	0.44-0.50 0.46±0.02 n=28	0.41-0.46 0.43±0.01 n=25	0.39-0.48 0.44±0.02 n=29	0.42-0.49 0.47±0.01 n=23	0.44-0.52 0.47±0.01 n=222
Postfemur (mm)	8.84-10.74 9.89±0.42 n=63	8.84-10.74 9.59±0.40 n=28	8.43-10.61 9.50±0.64 n=25	8.98-10.74 9.84±0.43 n=29	7.89-10.34 9.30±0.59 n=23	7.75-10.61 9.24±0.49 n=222
Tegmen / postfemur	1.27-1.56 1.41±0.06 n=63	1.29-1.53 1.39±0.06 n=28	1.38-1.70 1.54±0.08 n=25	1.31-1.67 1.52±0.09 n=29	1.14-1.41 1.30±0.06 n=23	1.18-1.55 1.35±0.06 n=222
Pronotum / postfemur	0.28-0.35 0.32±0.02 n=63	0.29-0.35 0.32±0.02 n=28	0.30-0.34 0.32±0.01 n=25	0.30-0.35 0.32±0.01 n=29	0.29-0.36 0.32±0.02 n=23	0.28-0.38 0.33±0.01 n=222
Stridulatory pegs	60-131 104.7±11.9 n=63	59-108 83.9±11.8 n=28	68-102 85.9±9.2 n=25	54-77 66.9±6.8 n=21	87-131 113.0±12.6 n=23	88-144 112.9±12.3 n=154
Stridulatory pegs / postfemur	6.30-13.38 10.59±1.21 n=63	6.67-10.88 8.75±1.18 n=28	6.49-11.03 9.08±1.11 n=25	5.64-7.91 6.82±0.66 n=21	9.69-14.38 12.17±1.28 n=23	9.22-16.20 12.28±1.38 n=154

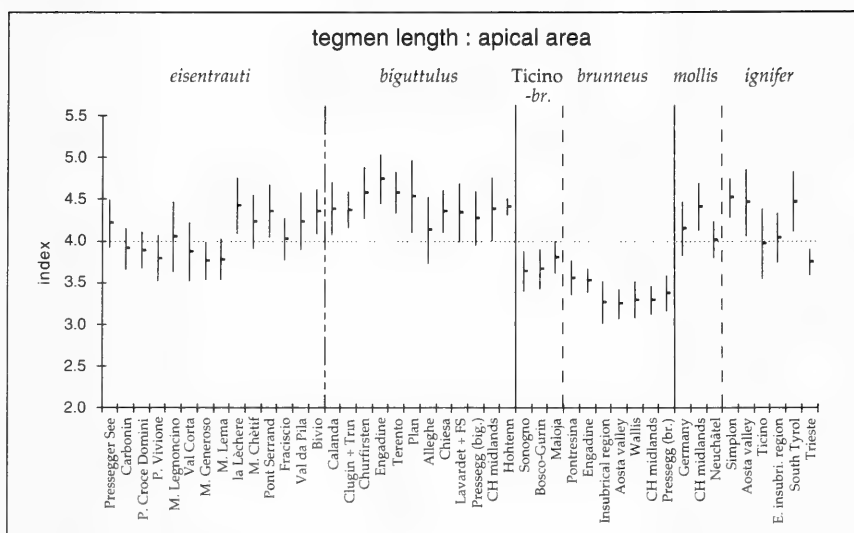


FIG. 8

Comparison of the index "tegmen length : length of apical area" in populations of the *C. biguttulus* group from the Alps and surrounding regions. Means and standard deviations are given.

Similar differences exist also between the population means of *C. brunneus* (0.06 - 0.07) and Ticino-brunneus (0.07 - 0.08). But, as with the former pair, variation is too great to allow assignment of single individuals. It is even impossible to discriminate between Ticino-brunneus and *C. mollis*.

Index "prozona: pronotum"

In all members of the *C. biguttulus*-group, the principal sulcus cuts the medial carina of the pronotum in the fourth tenth of the pronotal length (tab. 1-2). Differences between forms and populations are weak and variation is high, thus this character does not help in discrimination of the taxa. However there are some trends in individual populations worth of describing. The population means for *C. eisenrauti* and *C. biguttulus* vary between 0.44 and 0.46. It is striking that in most populations of *C. eisenrauti* it is almost exactly 0.46, only 4 populations deviate: the easternmost populations (Pressegger See and Carbonin) and to a lesser degree the Fraciscio population in which the index is higher (0.48 or 0.47 in the latter) and thus the same as in *C. mollis* and *C. m. ignifer*, and the Val da Pila population in which this index is lower (0.44) which agrees with the lower values of *C. biguttulus* but is also closer to the values of *C. brunneus*. In *C. brunneus* the population means vary between 0.42 and 0.44 except for the Engadine populations in which the index with 0.46 equals *C. eisenrauti* and *C. biguttulus*.

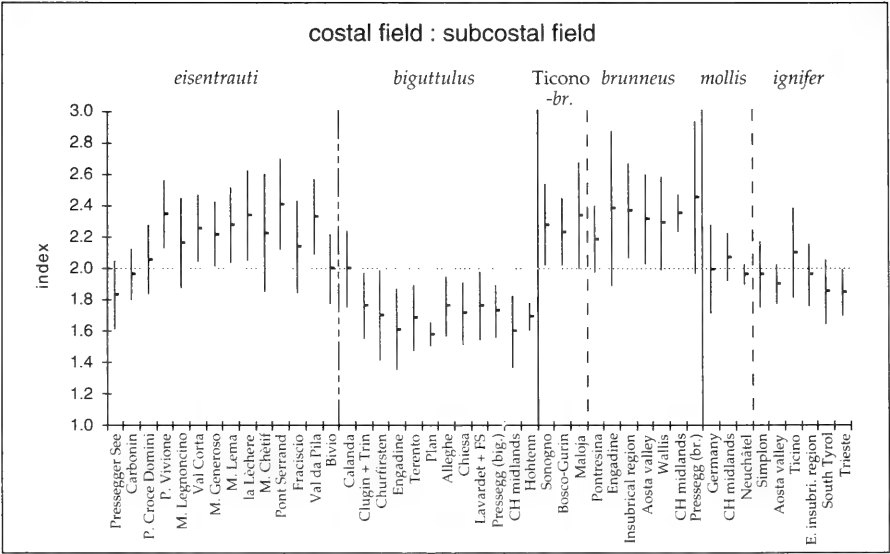


FIG. 9

Comparison of the index "width of costal field : width of subcostal field of tegmen" in populations of the *C. biguttulus* group from the Alps and surrounding regions. Means and standard deviations are given.

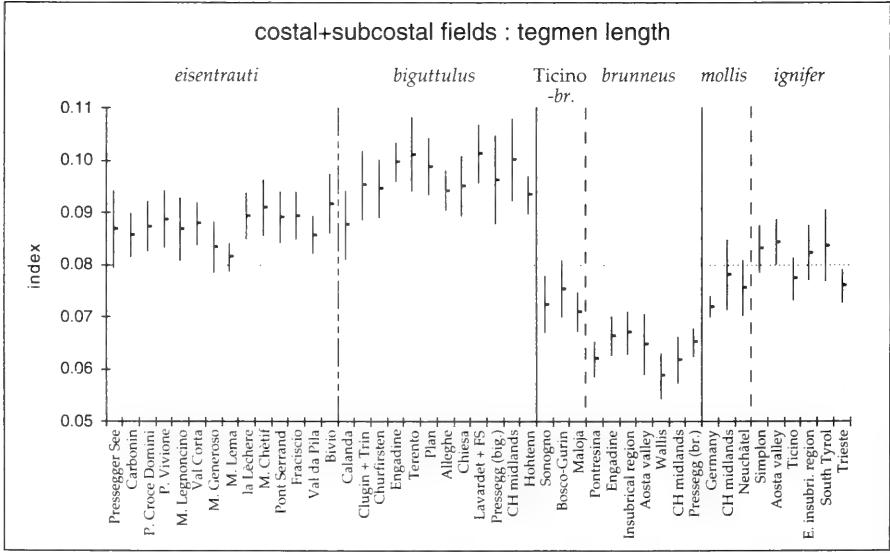


FIG. 10

Comparison of the index "combined width of costal and subcostal fields : tegmen length" in populations of the *C. biguttulus* group from the Alps and surrounding regions. Means and standard deviations are given.

Number of stridulatory pegs

The number of stridulatory pegs are often useful to discriminate between *C. brunneus* and other similar taxa (HARZ 1957, INGRISCH & PAVICEVIC 1985). Moreover, different ranges of peg numbers are described for *C. biguttulus* and *C. mollis* (HARZ 1957). In all specimens of *C. brunneus* and most specimens of the other taxa, the number of stridulatory pegs on the inner side of the postfemur was counted. The results however were surprising. With the exception of the nominate form of *C. brunneus*, the population means for most populations vary between 90 and 120, with a tendency that the means for *C. mollis* are at the upper end of this range, and for some *C. biguttulus* populations at the lower end of this range (fig. 11). Those differences however do not allow separation of the taxa. Relating the number of stridulatory pegs to the length of the postfemur does not suggest that the number might be correlated with body size: The index "number of stridulatory pegs: postfemur length" reflects exactly the same trends and the same differences between populations as the pure numbers.

Of greater interest are the great differences between populations within *C. brunneus*. Only in the populations from the Swiss midlands, Valais, Engadine (except

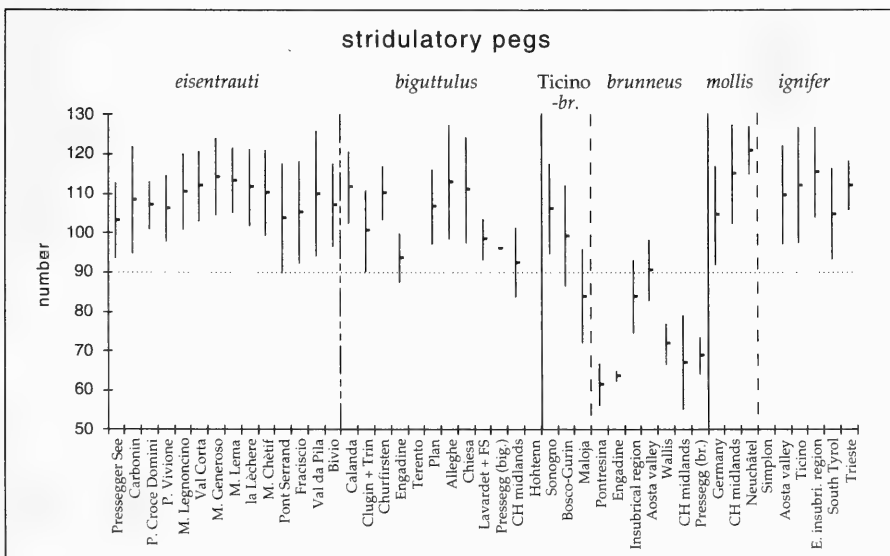


FIG. 11

Comparison of the number of stridulatory pegs in populations of the *C. biguttulus* group from the Alps and surrounding regions. Means and standard deviations are given.

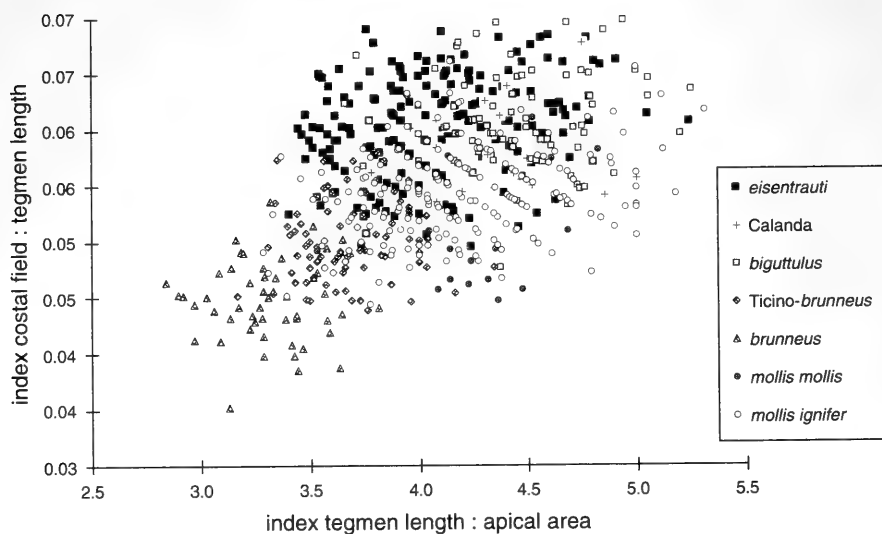


FIG. 12

Scatter diagram showing individual variation of grasshoppers of the *C. biguttulus* group in the Alps with regard to the indices "width of costal field: tegmen length" and "tegmen length: length of apical area".

Maloja) and Carinthia, the number of stridulatory pegs is below 80 as described for *C. brunneus brunneus*. In contrast, in *Ticino-brunneus* from Sonogno and Bosco-Gurin, the numbers of stridulatory pegs ([60 -] 78 -131) can be as high as in *C. mollis*, *C. eisentrauti* or *C. biguttulus*. Populations from Maloja, the Insubrical Region and the Aosta valley are intermediate, with numbers ([59 -] 68 -108) higher than in nominate *C. brunneus* but slightly lower than in the other taxa of the *C. biguttulus* group. The number of stridulatory pegs of the Maloja population was recently described as 98 - 116 (NADIG 1991). This value is slightly higher than in the specimens studied by myself.

Coloration

Apart from the characters which can be measured, there is a difference between the taxa concerning the coloration of the hind tibiae and the abdominal apex. This character however is most useful in live grasshoppers as some change of coloration occurs even in freeze-dried specimens. In *C. eisentrauti*, *C. mollis igniter*, *Ticino-brunneus* and the Pontresina population of *C. brunneus*, the posttibiae and the abdominal apex are always bright red in live grasshoppers. Apart from freshly moulted individuals, I have not yet seen a single exception. In museum specimens, the colour darkens and often changes to orange-brown. On the other hand in *C. biguttulus*, the remaining populations of *C. brunneus* and in *C. m. mollis*, the colour of

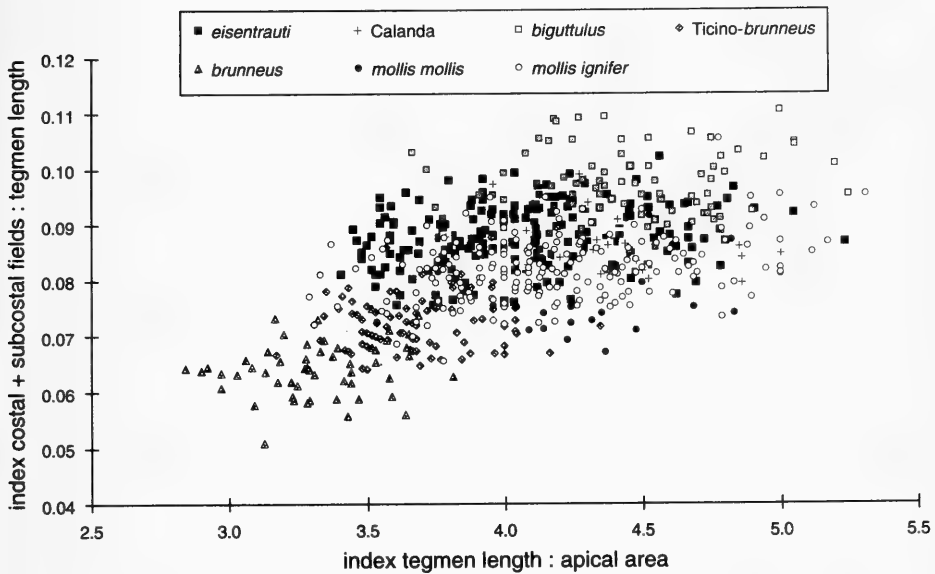


FIG. 13

Scatter diagram showing individual variation of grasshoppers of the *C. biguttulus* group in the Alps with regard to the indices "combined width of costal and subcostal fields : tegmen length" and "tegmen length : length of apical area". All taxa considered.

the posttibiae varies from yellowish brown to a light orange red, but is never so bright as in the southern forms. In museum specimens the colour looks yellowish, brownish or reddish. The colour can easily change into red if the tibiae come into contact with ethyl acetate or are kept in vapour of ethyl acetate for a prolonged period.

Multi-character comparisons

The preceding comparisons reveal that the taxa under study cannot be separated with certainty on the base of a single morphological character. Although the means may differ distinctly between taxa, variation is high and the ranges usually overlap to such an extent that it would be difficult to assign single specimens. It was thus tested, whether a set of characters allows discrimination between the taxa.

The characters discriminating best in the single character analysis were chosen for use in paired-characters analysis:

- width of costal and subcostal fields,
- index costal : subcostal field,
- index costal + subcostal fields : tegmen length,
- index tegmen length : apical area,
- index tegmen length : postfemur,
- number of stridulatory pegs.

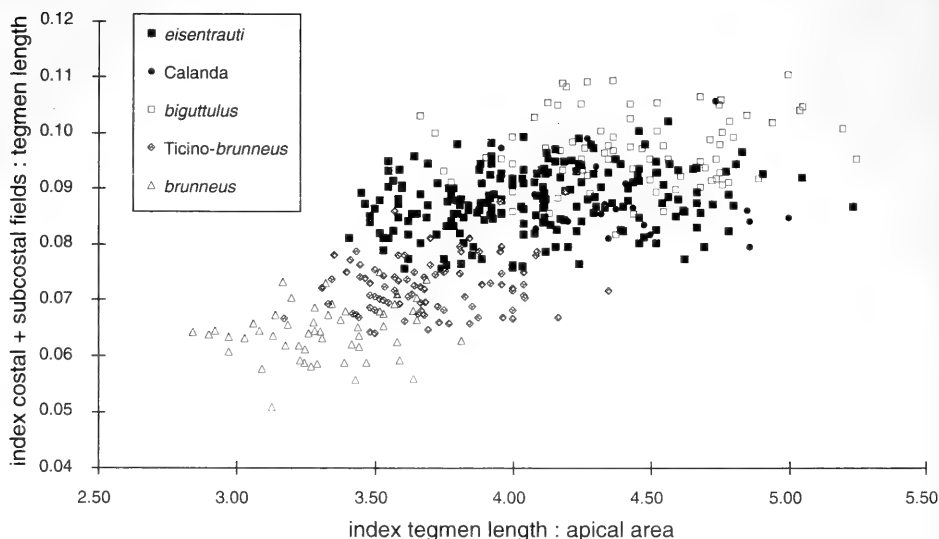


FIG. 14

Scatter diagram showing individual variation of grasshoppers of the *C. biguttulus* group in the Alps with regard to the indices "combined width of costal and subcostal fields : tegmen length" and "tegmen length : length of apical area". Analysis restricted to *C. biguttulus*, *C. eisentrauti*, *Ticino-brunneus* and *C. brunneus*.

All of those six characters were paired with each other. Most pairings did not seem any better than a single character analysis. Thus only the best discriminating pairings are described below.

Index "costal field : tegmen length" paired with index "tegmen length : apical area"

The dots drawn for the individuals of the different taxa concentrate in different areas of the scatter diagram (fig. 12). However the overlap between the different taxa is too high for clear lines to be drawn between them. Especially *C. biguttulus*, *C. eisentrauti* and *C. m. ignifer* overlap to such an extent that they can be treated as a single unit. Only dots drawn for individuals of nominate *C. brunneus* seem to be rather remote from the remaining. However they overlap with those for *Ticino-brunneus*, and those for *Ticino-brunneus* overlap with those for *C. eisentrauti* and *C. m. ignifer*.

Very similar results are obtained with the analysis of "width of costal + subcostal fields (in mm)" paired with the index "tegmen length : apical area".

Index "costal + subcostal fields: tegmen length" paired with index "tegmen length: apical area"

This analysis discriminates best between the different taxa. If we include all taxa in the analysis, the dots for the individuals of the different taxa concentrate in

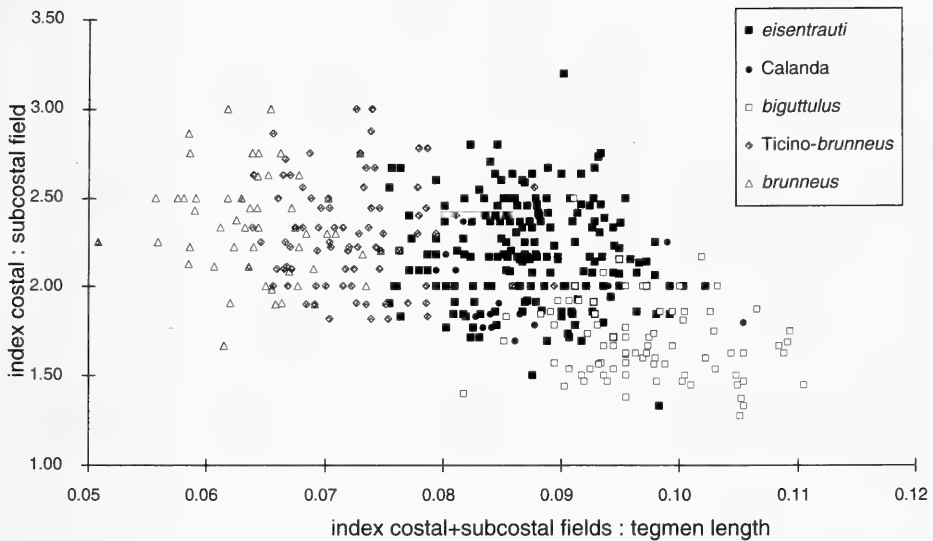


FIG. 15

Scatter diagram showing individual variation of grasshoppers of the *C. biguttulus* group in the Alps with regard to the indices "width of costal field: width of subcostal field" and "combined width of costal and subcostal fields: tegmen length". Analysis restricted to *C. biguttulus*, *C. eisenrauti*, Ticino-brunneus and *C. brunneus*.

different areas of the scatter diagram, but with a great deal of overlap between them (fig. 13). Thus wide zones of overlap exist between *C. biguttulus* and *C. eisenrauti*, between *C. eisenrauti* and *C. m. ignifer*, and between Ticino-brunneus and both *C. eisenrauti* and *C. m. ignifer*. The Calanda population of *C. biguttulus* falls completely within the range of *C. eisenrauti*, but practically all individuals fall into the zone of overlap between both taxa. Most individuals of *C. m. mollis* concentrate at the edge of the range of *C. m. ignifer*, but some fall within the range of any of the other taxa. The nominate form of *C. brunneus* is rather distinct from the other taxa except Ticino-brunneus, but overlaps to a some degree with *C. m. ignifer*.

If the analysis is reduced to include only the nominate forms of *C. biguttulus*, *C. brunneus* and *C. mollis*, the dots for the individuals of the three taxa cluster almost completely separately in different areas of the scatter diagram. There is however a weak overlap between the dots for *C. mollis* and *C. biguttulus* as well as between those for *C. mollis* and *C. brunneus*, whereas *C. brunneus* and *C. biguttulus* differ distinctly.

In a third step both forms of *C. mollis* were excluded from the analysis to make the relations between the remaining taxa more clear. This analysis shows that there is a gradual cline of both characters from *C. brunneus* via Ticino-brunneus and *C. eisenrauti* to *C. biguttulus*, with large zones of overlap between the neighbouring taxa (fig 14).

Index "costal + subcostal fields : tegmen length" paired with index "costal : subcostal field"

This analysis reveals exactly the same trend as the previous one. There is a gradual cline of the characters from *C. brunneus* via *Ticino-brunneus* and *C. eisen-rauti* to *C. biguttulus* (fig. 15). Individuals of the Calanda population fall completely within the range of *C. eisen-rauti*.

Ternary analysis

The three most distinctive indices "tegmen length : apical area", "costal- and subcostal fields : tegmen length" (multiplied by factor 100 to bring it in the same size with the other indices), and "costal field : subcostal field" were plotted on a triangular graph. It was impossible to identify any of the taxa on the graph, even if only pairs of taxa were compared. Although the dots for the different taxa centred in slightly different areas of the triangular graph, the clusters overlapped almost completely. I thus abstain from presenting the graph.

Conclusion

Summarising the morphological investigations, the conclusion may be drawn that it will be impossible to identify every single individual of the *C. biguttulus*-group with certainty on the base of morphological characters alone. However, as the means of several characters distinctly deviate between taxa, identification of series of individuals might be possible with enough certainty for most populations. The question now arises whether the behavioural characters, i.e. stridulation, are diversified enough to function as an isolating barrier between the taxa.

STRIDULATION

Stridulation of *C. biguttulus*, *C. brunneus* and *C. mollis* are distinct enough to recognise the species without aid, and the statistical analysis thus concentrates on possible distinctions between *C. biguttulus* and *C. eisen-rauti*, between *C. brunneus* and *Ticino-brunneus*, and between *C. mollis* and *C. mollis ignifer*. The first pair of taxa yield by far the most obvious problem and is thus dealt with in greatest detail.

Chorthippus biguttulus and C. eisen-rauti

Chorthippus biguttulus (LINNÉ, 1758)

The song of nominate *C. biguttulus* consists typically of three crescendoing verses, of which the first is distinctly longer than the second and third (fig. 16A). The differences in relative duration of first and second verse vary within populations, but also regionally. Jacobs (1964) found relatively short first verses in populations from Schleswig-Holstein-Jutland (North Germany - Denmark) and in local populations in

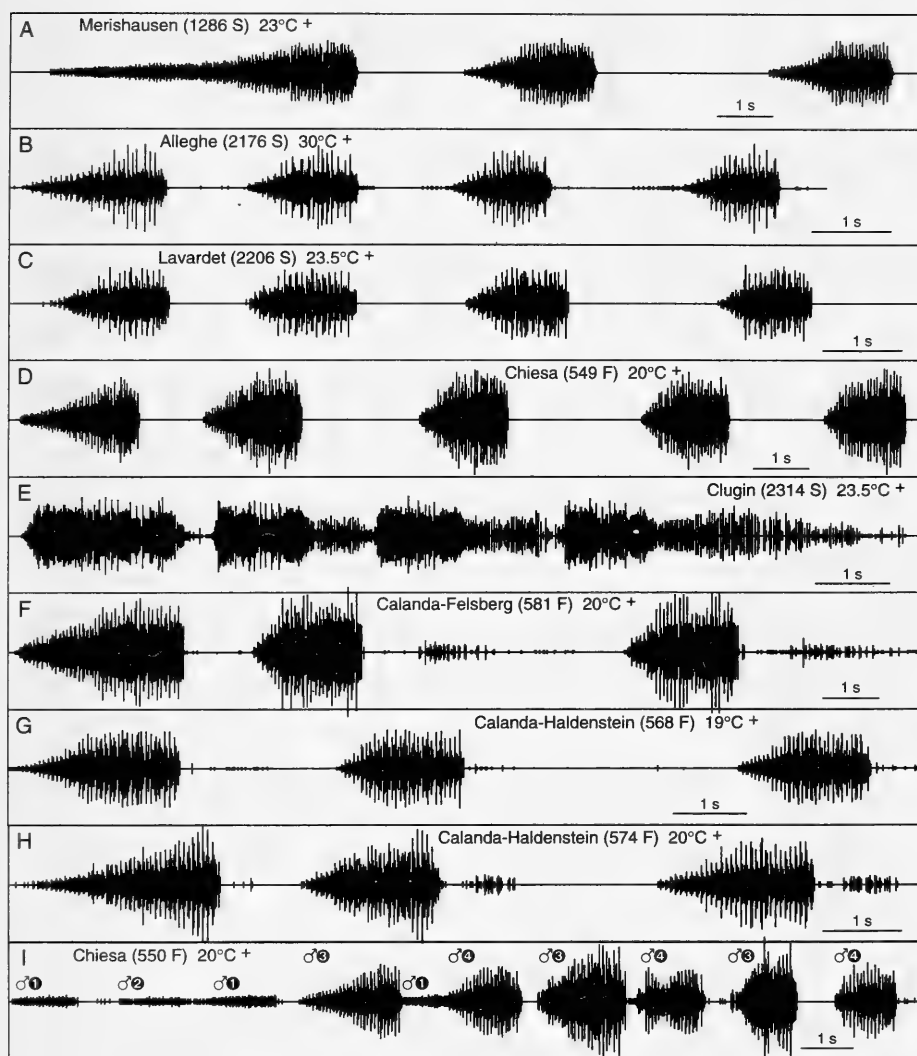


FIG. 16

Oscillograms of stridulation of *C. biguttulus* from different localities of the Alps and the Swiss midlands. A-I: Complete songs. Oscillogram E shows an extremely long buzzing following the verses; buzzing can also be noticed in oscillograms F - H. Oscillogram I shows mixed singing of a group of 4 males (different males marked with different numbers).

The numbers (in brackets) following the locality indicate the record number; F = field, S = studio recording. The "+" following the ambient temperature indicates that the recordings were done with males warming up in sunshine or near a 60 Watt bulb.

the French Pyrenees and the French Alps, and relatively long first verses in the southeastern Alps (Carinthia and Steiermark). The latter finding contrasts with the results of the present study that in the nearby regions of northeastern Italy (Veneto, Carnia) the differences between first and second verse are less striking. In the southern alpine populations, the number of verses per song was often higher than three even in isolated males (fig. 16B-D), while in other populations their number usually increased only during courtship or rivalry.

In the field, several males are often singing at the same time. Then, usually the rather quiet beginning of the verse of the second male coincides with the loud final part of the verse of the first male and so on. However, in the southern alpine populations with shorter verses, the males may sing alternately with the verses of each male falling into the pauses of the other (fig. 16I).

The verses are composed of a variable number of echemes, and each echeme consists typically of three syllables (fig. 17C). The subdivision of the verses into echemes results from the fact that after the initial complete downstroke of the hind femur, it is raised stepwise with somewhat incomplete up and down movements. It reaches its initial high position only in the last syllable of an echeme (Elsner 1974). As a result the first pulse of an echeme, produced by the long downstroke, is usually louder than the following (fig. 17C-F). The time pattern of the syllables is most distinct in one-leg stridulation (fig. 17C-F). Normal males try to camouflage the small gaps between the syllables by slightly asynchronous movements of both hindlegs (ELSNER 1974, HELVERSEN 1972). Moreover, the males try to mask the pauses between the echemes by a prolonged upmovement of the hindleg in the last syllable of an echeme.

The number of three syllables per echeme is rather constant in *C. biguttulus* populations living north of the Alps, but subject to greater variation in the southern alpine populations (see below).

The Calanda population of *C. biguttulus*

Despite of the morphological difference, there is no general difference in stridulation between the Calanda population and nominate *C. biguttulus* (figs. 16F-H, 17D). It may however be noticed that many males produced a very distinct quiet buzzing following the verses (fig. 17A). This is produced by a rather slow, incomplete down-and-up movement of the hind femur, such that single pulses appear even in less time-expanded oscillograms. This buzzing however was even more expressed in some males of nominate *C. biguttulus* from Clugin, in which it filled the pauses between two successive verses completely (fig. 16E, 17B). The buzzing was also very distinct in the *C. eisentrauti* population of Bivio. A weak buzzing was produced by males from several populations, it was however never as strong as in those three populations. The Calanda, Clugin and Bivio populations live in a rather restricted area in Grisons from the Upper Rhine valley to the Engadine. The buzzing is thus a local curiosity. It possibly indicates some gene flow between populations of *C. biguttulus* and *C. eisentrauti* in this area.

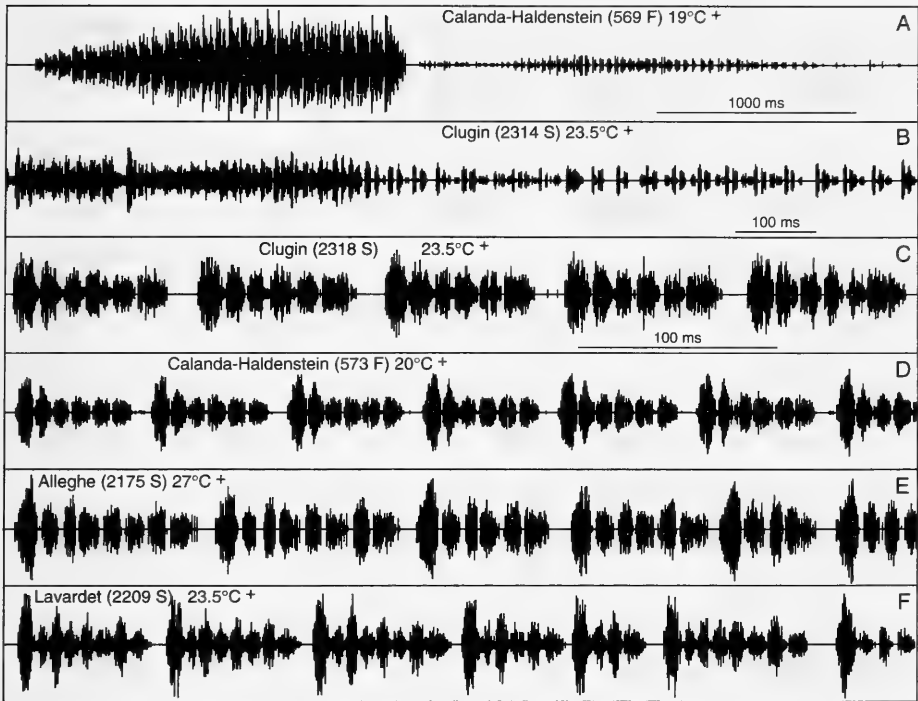


FIG. 17

Oscillograms of stridulation of *C. biguttulus* from different localities of the Alps. A: Single verse followed by extended buzzing; B: End of last verse and beginning of buzzing sound at a greater time scale; C-F: Sectors of verses of one-leg-stridulation to show syllable patterns of echemes.

Chorthippus eisentrauti (RAMME, 1931)

The song is principally the same as in *C. biguttulus* with the following deviations: The verses are usually much shorter with the first and second verse of subequal length. Instead, the number of verses per song is higher, and 4 - 8 verses are commonly heard (fig. 18). Generally, verse duration was longest in the populations from the Aosta valley, but also in some males from Bivio and from Pressegger See (type locality). The shortest verses occurred in the populations from Ticino (Mt. Generoso and Mt. Lema) and in some males from Fraciscio and Val da Pila (the latter southwest of the Maloja-pass). Although verse duration was variable in all populations, it was extremely variable in the Fraciscio population in which it was almost as short as *C. brunneus* in some males and almost as long as *C. biguttulus* in others (fig. 18G-I).

If two males sing together in the field, their verses often alternate, i.e. one male sings in the pauses of the other (fig. 18C). However in males producing longer verses, the verses overlap, i.e. the second male starts singing before the first has ended.

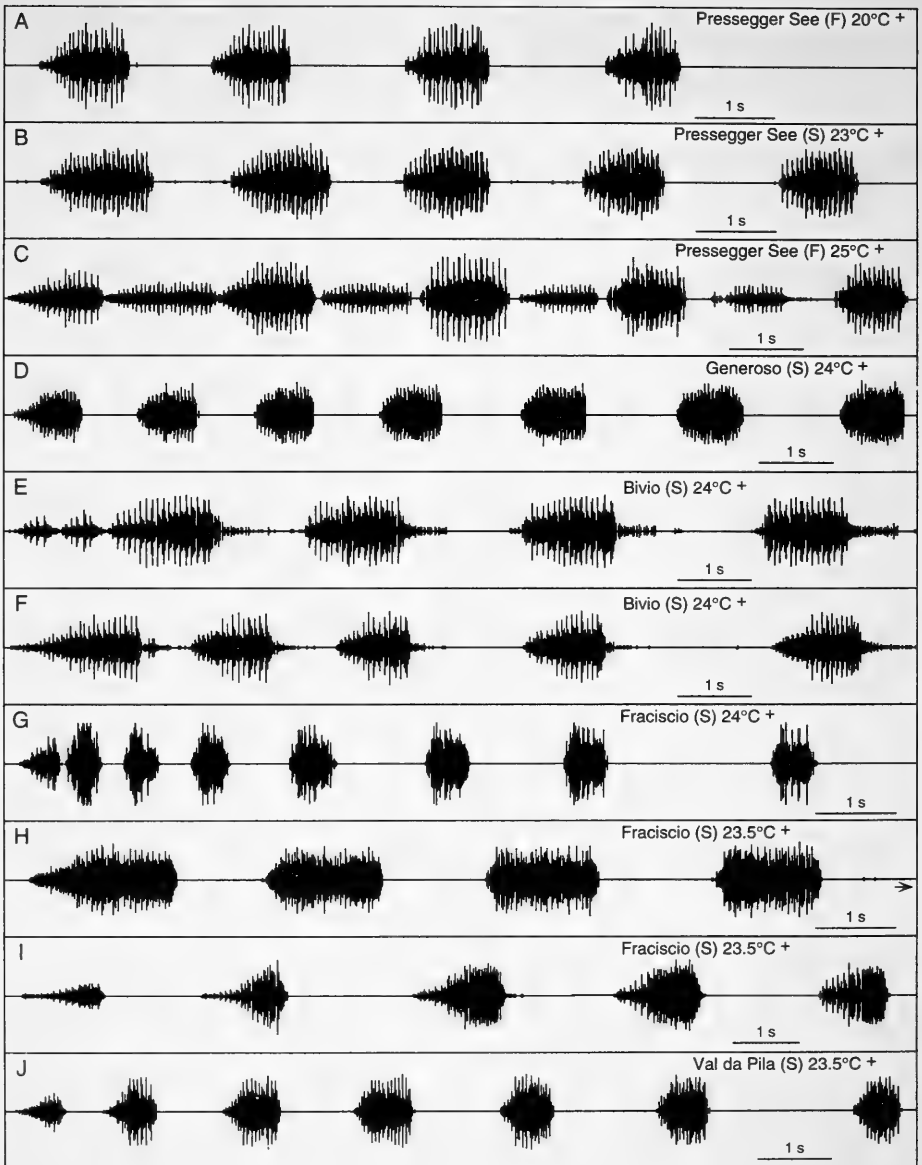


FIG. 18

Oscillograms of stridulation of *C. eisentrauti* from different localities of the Alps to show the variability of the song pattern within and between populations. A-G, I-J: Complete songs; C: Response songs of two males (recognisable by different amplitude); E: Verse interruption of the first verse and buzzing following the verses. H: Only the first four of eight verses shown.

The verses are composed of echemes in the same way as in *C. biguttulus*. The number of syllables per echeme, however, are very variable (fig. 19). Often the verse starts with low-syllable echemes (2-3 syllables) and ends with high-syllable echemes (up to 44 syllables), but as often the syllable number can also be rather constant or irregularly fluctuating throughout the verse. In many populations, the syllable pattern of the echemes varied between the males or even in the same male in successive songs or verses. Fig. 19E-F shows two syllable patterns produced by the same male on successive days.

Usually the first pulse per echeme is louder than the following as in *C. biguttulus* (fig. 19A-C). However some of the long echemes consist of uniform syllables with a loud downstroke and a rather quiet upstroke (fig. 19D, H), thus resembling the situation in *C. mollis*. The corresponding leg movement however was not recorded. A male can change the pattern even within a verse (fig. 19G).

As curiosities males produced one or several very quiet "preverses" before starting with the first normal verse. Those preverses were either unstructured or displayed the same echeme-syllable pattern as normal verses. Preverses most commonly occurred in the following populations: Passo di Croce Domini, Mt. Legnoncino, Val Corta, Fraciscio, Bivio, and all populations of the Aosta valley; occasionally they were also produced by males from Pressegger See, Carbonin, Passo Vivione, Mt. Lema and Val da Pila.

Another deviation from the normal song pattern was a "multi-interruption" of the first verse (fig. 18E). Interruption of the first verse can occasionally also occur in nominate *C. biguttulus* in any part of the verse. In *C. eisentrauti*, it occurred always at the beginning of the verse, where short units were separated by an interruption. This was actually not a real pause. The verse seemed to stop, but the male immediately started singing again. However the distinction between preverses, separated by a distinct pause from the first loud verse, and verse interruption was gradual. Occasionally, males produced both preverses and verse interruption. Verse interruption was recorded from males of the following populations: Bivio, Fraciscio, Mt. Lema and occasionally of males from Carbonin.

A buzzing following the verses, as already described under the Calanda population, was most obvious in the Bivio and Pont Serrand populations (fig. 18E-F), but occurred occasionally also in songs of males from Fraciscio and Val da Pila.

Statistical analysis of the song characters

The ranges, means and standard deviations for all song parameters and calculations of indices are summarised for regional populations in tab. 3.

Number of verses per song and verse duration

The verses of *C. eisentrauti* are usually shorter but more numerous per song than in *C. biguttulus*. The number of verses per song is more variable in *C. eisentrauti* than in *C. biguttulus* as revealed by the greater standard deviations (fig. 20). In the

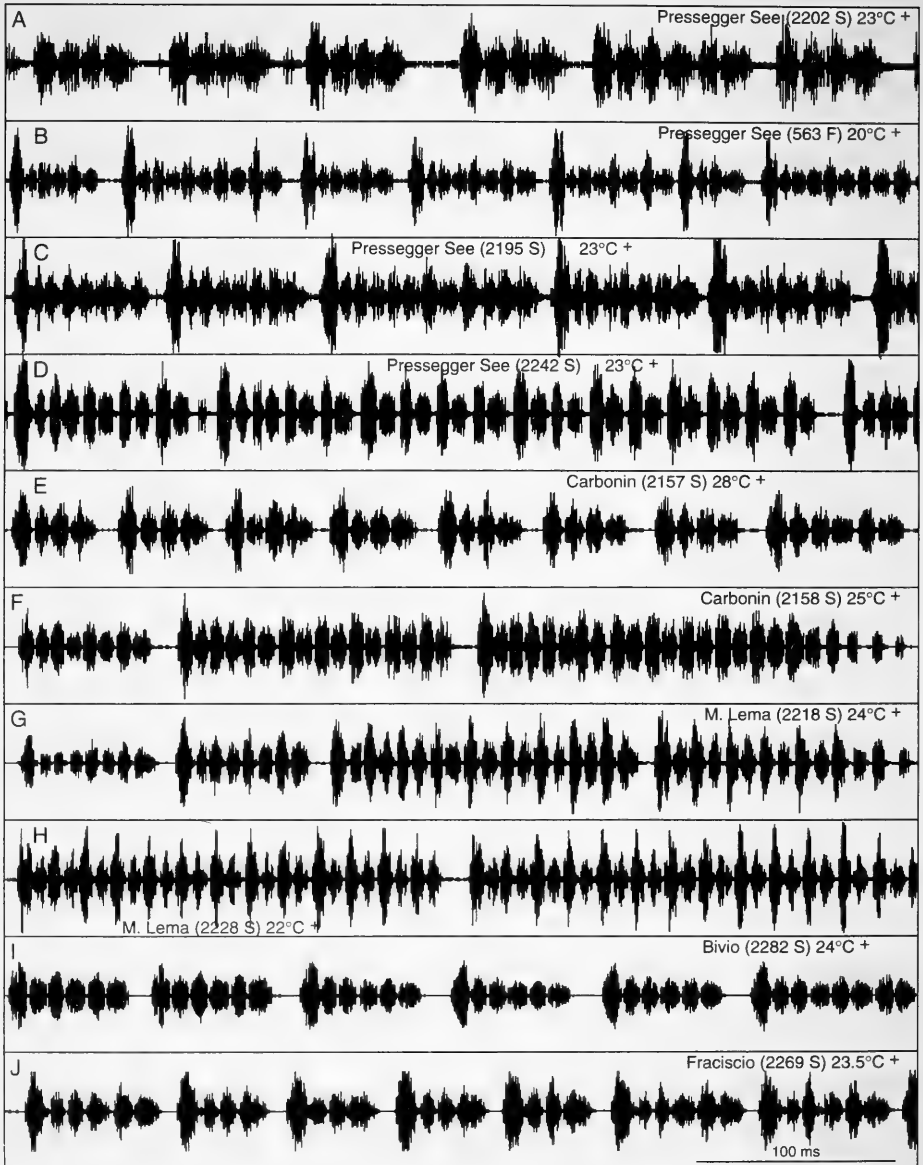


FIG. 19

Oscillograms of stridulation of *C. eisentrauti* from different localities of the Alps. A-J: Sectors of verses of one-leg-stridulation to show variation of syllable patterns of echemes. E and F were produced by the same male on successive days.

TAB. 3

Song characters of the *C. biguttulus* - *eisentrauti* complex. Minimum, maximum, mean, standard deviation and number of observations are given. Local populations are clustered to regional groups to reduce the number of data. Units are counts, msec, or index values. Data in round brackets refer to units, e.g. (msec), in square brackets to base of calculation, e.g. [syllables] = index based on number of syllables per verse; [msec] = index based on duration in msec.

	<i>eisentrauti</i>				<i>biguttulus</i>		
	Pressegger See Carbonin	Insubrial Region	Aosta valley	Bivio	Calanda	CH midlands, Valais, Engadine	South Tyrol, Veneto, Carinthia
Verses per song	1-9 4.4±1.6 n=143	2-16 6.2±2.3 n=292	3-11 6.1±1.7 n=65	2-12 4.1±1.6 n=57	1-9 2.81.1 n=105	2-7 3.9±1.3 n=61	1-8 3.7±1.5 n=126
Echemes per verse	4-47 14.3±5.6 n=628	1-41 12.9±5.3 n=1821	3-56 22.8±6.6 n=397	4-36 16.9±5.1 n=237	10-74 28.5±10.7 n=290	10-67 23.9±9.0 n=240	8-78 24.8±9.3 n=458
Syllables per echeme	1-44 3.1±1.2 n=9307	1-44 3.1±1.6 n=23559	1-11 2.2±0.5 n=9092	1-12 3.2±0.8 n=4035	1-11 3.1±0.5 n=8253	1-21 3.2±1.1 n=6229	1-21 3.3±0.9 n=10841
Syllables per 1st verse	16-136 48.4±21.6 n=143	6-92 39.6±14.3 n=292	22-113 53.9±21.4 n=65	16-106 66.0±19.7 n=57	44-225 112.1±39.9 n=106	39-252 120.2±46.3 n=61	20-234 106.4±40.7 n=126
Syllables per follow. verses	16-91 42.5±12.4 n=486	12-75 40.5±9.5 n=1529	28-77 48.9±9.2 n=332	18-89 50.7±10.7 n=180	22-119 73.4±15.6 n=185	36-111 68.0±15.9 n=179	21-102 71.2±14.2 n=333
1st / 2nd verse [syllables]	0.29-2.13 1.06±0.27 n=141	0.21-2.35 0.96±0.27 n=292	0.50-1.77 0.98±0.27 n=65	0.31-2.65 1.37±0.46 n=57	0.55-9.27 1.55±0.97 n=102	0.48-3.50 1.68±0.57 n=61	0.69-3.41 1.42±0.46 n=123
Verse duration (msec) [1st verse]	384-2906 1163±481 n=143	196-4781 1036±473 n=293	952-3156 1626±516 n=66	393-2237 1460±410 n=57	1025-6218 2480±920 n=105	1018-8734 2992±1393 n=61	543-5375 2476±941 n=125
Verse duration (msec) [following v.]	403-2231 1049±298 n=486	279-2351 1013±327 n=1528	837-2383 1478±315 n=330	478-1887 1110±221 n=180	681-2637 1640±322 n=185	899-2912 1666±413 n=179	542-3144 1654±449 n=330
1st / 2nd verse [msec]	0.28-2.01 1.06±0.25 n=141	0.29-2.78 1.00±0.27 n=292	0.55-1.94 1.02±0.27 n=65	0.27-2.14 1.35±0.41 n=57	0.58-6.95 1.53±0.81 n=102	0.45-3.93 1.71±0.60 n=61	0.77-3.29 1.45±0.46 n=122

Pressegger See and the Bivio populations the mean number of verses per song is about 4, while in the other populations of *C. eisentrauti* the means are between 5 and 8. In most populations of *C. biguttulus* the mean number of verses per song is about 3, but about 4 in the populations from Clugin, Engadine and Terento, and almost 5 in the Lavardet population. The comparison confirms that there tends to be a difference in the verse number between the two taxa, but the within-taxa variation is too large for this difference to be used as a character for separating the taxa.

Analysing the verse duration, the values for the first and the following verses of a song have been calculated separately, as the first verse can be distinctly longer than the following. To exclude the effect of temperature on the speed of stridulation from the analysis, the number of syllables, i.e. down and upstrokes of the hind femur, was used as the main measure for the verse length. All calculations have also been done with the actual duration in milliseconds. Both analyses revealed the same trend.

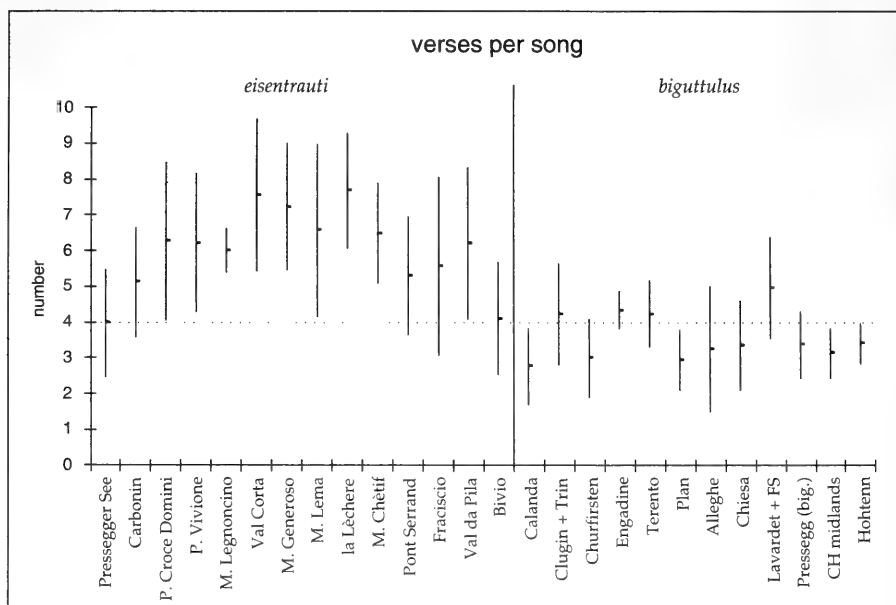


FIG. 20

Number of verses per song in populations of *C. biguttulus* and *C. eisentrauti* from the Alps. Means and standard deviations are given.

The mean numbers of syllables per first verse in populations of *C. eisentrauti* varied between 25 and 67 (fig. 21). It was highest in the Bivio (mean 66) and the Pont Serrand (mean 67) populations, 53 in the population from Pressegger See and below 50 in all other populations. In *C. biguttulus* the mean numbers of syllables per first verse were distinctly higher. The mean values varied between 82 in the Lavardet and 183 in the Hohtenn population. The syllable numbers varied to a greater degree within populations of *C. biguttulus* than within populations of *C. eisentrauti*. Although this character allows separation of the population means of both taxa, there is a great deal of overlap between individuals, namely from populations of *C. eisentrauti* with a rather high syllable number (Pont Serrand and Bivio) with those of *C. biguttulus* with a rather low number of syllables (Lavardet and Chiesa). The mean for the Calanda population is 112.

The mean of the absolute verse duration of the first verse of *C. eisentrauti* was lowest in the population from P. Croce Domini (632 ms) and highest in the population from Pont Serrand (1883 ms), in the other populations the means varied from 800 to 1600 ms (1250 ms at the type locality). In *C. biguttulus*, the means of the absolute duration of the first verse were distinctly higher. They were lowest in the populations from Lavardet (2026 ms) and Chiesa (2159 ms), highest in Hohtenn (4369 ms) and

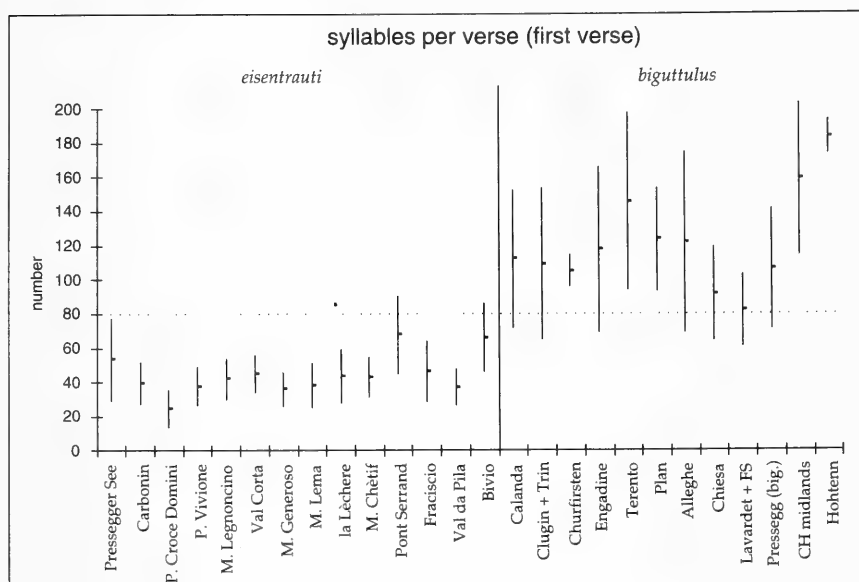


FIG. 21

Number of syllables in the first verses of songs of *C. biguttulus* and *C. eisentrauti* from the Alps. Means and standard deviations are given.

the Swiss midlands (3820 ms), the means of the other populations varied between 2500 and 3200 ms. The mean for the Calanda population was 2480 ms. Although the means differ between *C. biguttulus* and *C. eisentrauti*, individual variation is even greater than when using the number of syllables as a measure for the verse length. Single individuals thus cannot be identified on the base of this character alone.

The population means of the number of syllables in the following verses varied in *C. eisentrauti* between 35 (P. Croce Domini and Generoso) and 55 (Pont Serrand), with 46 in the type locality (tab. 3). In *C. biguttulus*, it varied between 64 (Lavardet and Clugin) and 89 in the Swiss midlands. The mean for the Calanda population was 73.

Using the syllable number as a measure for the verse duration, the population means thus differ between *C. eisentrauti* and *C. biguttulus*. This is not so when the absolute duration is compared. The population means for the duration of the following verses varied in *C. eisentrauti* between 817 ms (Mt. Generoso) and 1157 ms (Val Corta), with 1112 ms at the type locality. There are however four exceptions. The means for the three populations from the Aosta valley varied between 1397 ms and 1623 ms, and on Mt. Legnolino the mean was even 1644 ms. The latter values are the same as the population means for *C. biguttulus*. Those varied between 1568 ms (Chiesa) and 1974 ms (Swiss midlands). The mean for the Calanda population was 1640 ms.

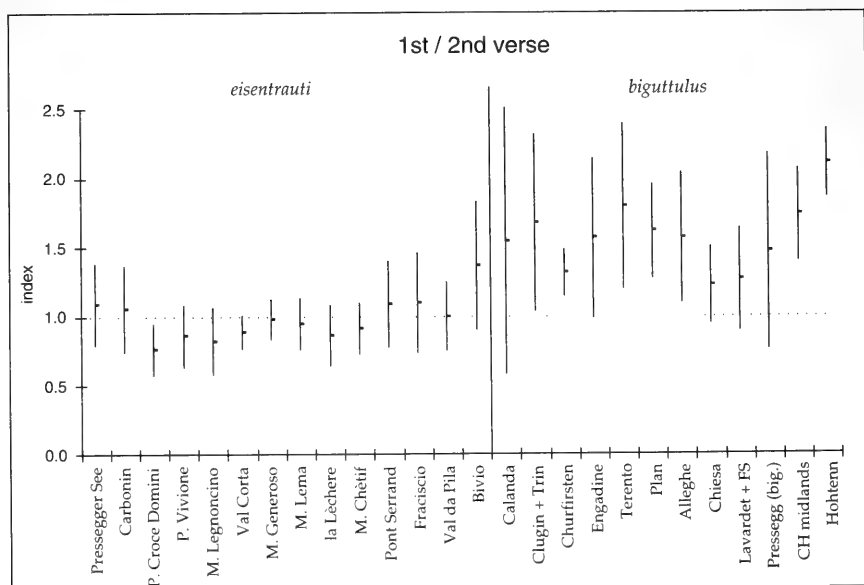


FIG. 22

Variation of the index "duration of the first: duration of the second verse" in songs of *C. biguttulus* and *C. eisentrauti* populations from the Alps. Means and standard deviations are given.

As the long verse durations of the four *C. eisentrauti* populations are not reflected in a higher number of syllables, it cannot be excluded that low temperature or low radiation had caused the long song durations. The recordings on Mt. Legnoncino were mainly made in the field during slightly misty weather conditions. Only males from Pont Serrand produced a rather high number of syllables per verse, and the long verse duration was thus to be expected.

An index "duration of first : duration of second verse" was calculated on the base of the number of syllables per verse. The population means for *C. eisentrauti* varied between 0.82 (P. Croce Domini) and 1.13 (Pont Serrand and Fraciscio), the mean for the Pressegger See population was 1.09 (fig. 22). That means that the first verse in a song is of about the same length as the second. The absolute variation of this index however was much higher: it varied between 0.27 and 2.78. Moreover, there is one exception. The mean of the population of Bivio was 1.35 and thus higher than the lowest population mean of *C. biguttulus*. In this species, the means varied between 1.27 (Chiesa) and 2.10 (Hohtenn). That means that in *C. biguttulus* the first verse of a song is usually between one third longer than and twice as long as the second. Total variation however was from 0.45 - 6.95 times longer than the second. The mean for the Calanda population was 1.53.

The Pressegger See populations

At the type locality of *C. eisenrauti*, Hermagor in Carinthia, this taxon lives in close proximity to nominate *C. biguttulus*, as already stated by RAMME (1931), FABER (1957) or SCHMIDT (1978). During my own visits, *C. eisenrauti* with the typical, striking red coloration of the tibiae and the abdomen, and the short duration of the verses was only found on the slopes of the mountain (Seeblickfelsen) above the village Pressegger See between NN+800 and NN+1500 m. It occurred on well insolated limestone cliffs that were scattered on a steep southerly exposed slope which was otherwise covered with pine forest. Another locality was along the forest road on the same mountain that leads up to the Rote Wand. In the latter place it occurred syntopically with *C. brunneus*. The lowest elevation at which *C. eisenrauti* could be found was the upper rim of a now unused quarry at the foot of the Seeblickfelsen. Within the quarry and at other places at the foot of the mountain, nominate *C. biguttulus* occurred. Two individuals from the base of the quarry however have the wing venation almost as in *C. eisenrauti* (compare figs. 3) but lacking the striking coloration of the hind tibiae. Their songs were those of nominate *C. biguttulus*, however, with a syllable pattern of *C. eisenrauti*. It thus cannot be excluded that occasional hybridisation between *C. biguttulus* and *C. eisenrauti* occurs at the type locality.

On the other hand, the population means of all characters that differed between *C. eisenrauti* and *C. biguttulus*, also differed between both populations from Pressegger See quite distinctly, although the ranges overlapped (figs. 20-23). This makes it unlikely that *C. eisenrauti* is but a local variant of *C. biguttulus*.

Syllable pattern of the echemes

In *C. biguttulus*, the by far most common number of syllables per echeme was three. Males from the Swiss midlands, Valais, Calanda and Engadine produced fewer than 10% echemes with more or with fewer syllables than three (fig. 23). In the southern alpine populations and *C. biguttulus* from Clugin, the percentage of echemes with four or more syllables increased to 17 - 32% of all syllables produced (fig. 23). In *C. biguttulus* from Lavardet, Chiesa, Alleghe and Clugin also the percentage of echemes with only two syllables was higher (5 - 11%).

In *C. eisenrauti*, the number of syllables per echeme was more variable than in *C. biguttulus*. In nine of the 14 populations studied, echemes with three syllables were the most common as in *C. biguttulus*, but the percentage of echemes with only two or with four and more syllables was distinctly higher (fig. 23). Males of the three populations from the Aosta valley and those from Mt. Legnoccino and Val Corta produced mainly two-syllabic echemes (63 - 92%). In those populations, the percentage of echemes with 4 or more syllables was accordingly low. In the remaining populations, the percentage of echemes with 4 or more syllables varied between 10 - 42% and was highest on Mt. Lema and Passo di Croce Domini.

As the stridulation of *C. eisenrauti* can consist of both echemes with less syllables and echemes with more syllables than in the stridulation of *C. biguttulus*, the

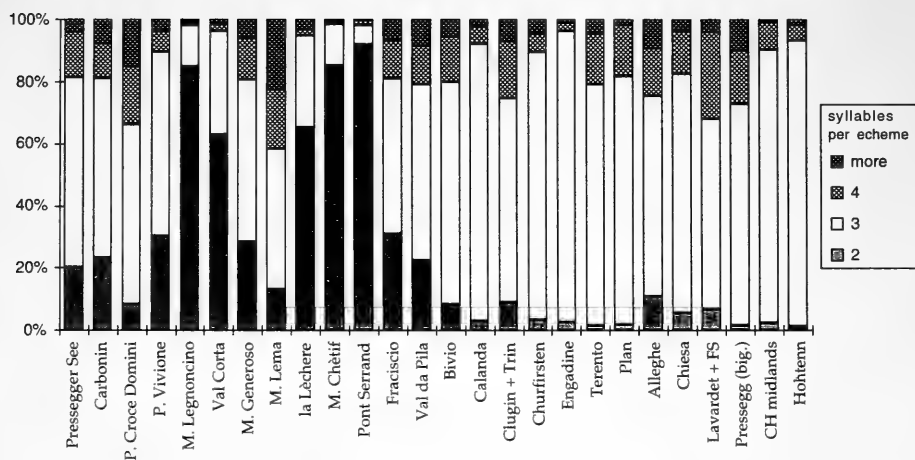


FIG. 23

Variation of the number of syllables per echeme in populations of *C. biguttulus* and *C. eisentrauti* from the Alps.

syllable pattern alone is possibly not a very important character in species recognition. At least, the character is not useful for separating *C. eisentrauti* from *C. biguttulus*.

Paired character analysis

Two sets of paired characters were used to test whether a combination of characters would allow to separate *C. eisentrauti* from *C. biguttulus*: (1) the number of syllables per first verse of a song (used as a measure for the syllable duration) paired with the number of verses per song (fig. 24) and (2) the same first character paired with the index "duration of first : second verse" (fig. 25).

Both analyses gave similar results. Although the majority of the dots for the stridulation of *C. eisentrauti* and *C. biguttulus* clustered in slightly different areas of the scatter diagrams, there is such a big overlap between both taxa that even a character set does not allow the separation of single specimens of either taxon. That means there is a gradual transition in behavioural characters, and the difference between the two taxa is merely a statistical difference of the means.

Conclusion

In summary, the main differences in the stridulation of *C. eisentrauti* compared with *C. biguttulus* are a shorter verse duration, a greater number of verses per song and a less regular syllable pattern of the echemes. All those differences concern however mainly the population means. Considering total variation, there is a great zone of overlap between both taxa. Recent studies proved that all parameters of the

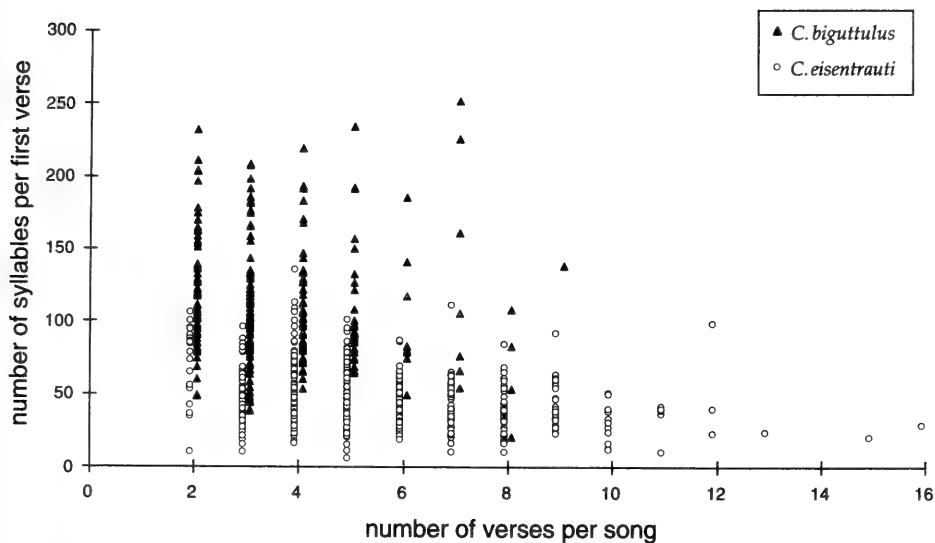


FIG. 24

Scatter diagram showing individual variation of the song parameters "number of syllables per first verse" and "number of verses per song" in populations of *C. biguttulus* and *C. eisentrauti* from the Alps.

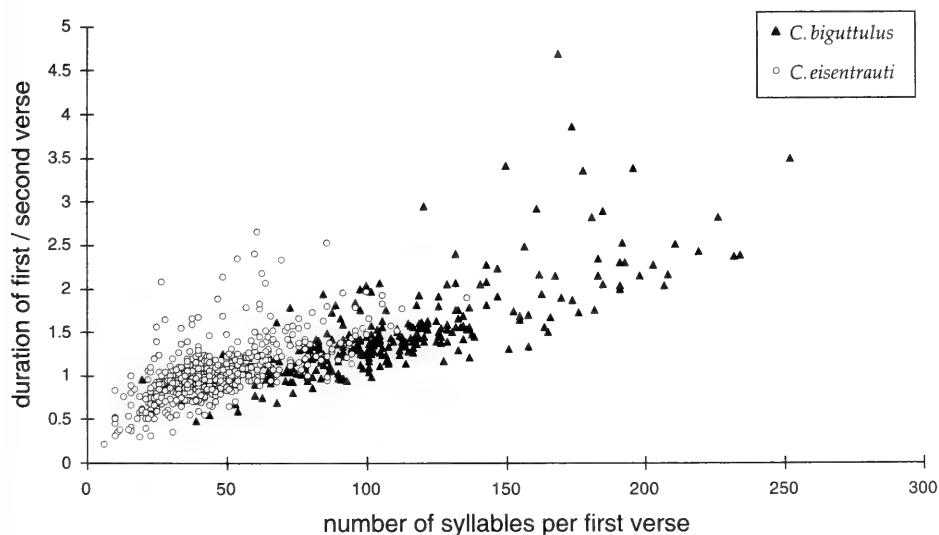


FIG. 25

Scatter diagram showing individual variation of the song parameters "index duration of first: duration of second verse" and "number of syllables per first verse" in populations of *C. biguttulus* and *C. eisentrauti* from the Alps.

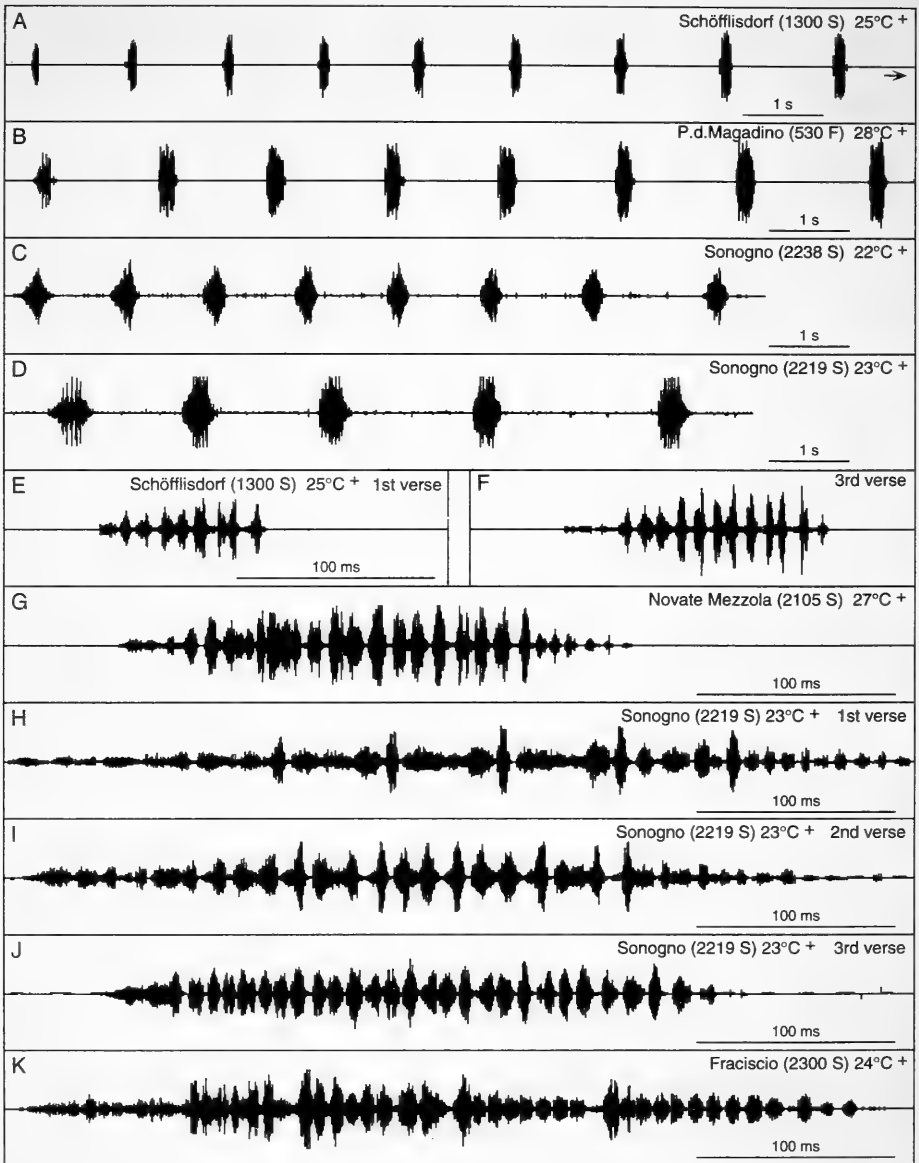


FIG. 26

A-J: Oscillograms of stridulation of *C. brunneus* from the Alps and the Swiss midlands. A-D: Complete songs; E-J: Single verses on a greater time scale; A-B, E-G: *C. brunneus*; C-D, H-J: Ticino-*brunneus*; K: One of the shortest verses produced by a *C. eisentrauti* male from Fraciscio.

TAB. 4

Song characters of *Chorthippus brunneus*. Minimum, maximum, mean, standard deviation and number of observations are given. Local populations are clustered to regional groups. Units are counts or msec.

	<i>brunneus</i>		<i>Ticino-brunneus</i>	
	Swiss midlands, Valais, Engadine, Carinthia	Insubrical Region, Aosta valley	Maloja	Sonogno, Bosco-Gurin
Verses per song	5-12 7.2±1.9 n=31	2-11 5.8±1.9 n=47	6-8 7.1±0.7 n=7	4-14 6.4±2.0 n=38
Pulses per first verse	5-17 11.5±3.2 n=31	6-26 15.7±5.4 n=47	10-22 14.9±4.6 n=7	16-42 26.6±7.5 n=38
Pulses per following verses	6-21 13.8±2.5 n=190	8-29 19.3±4.2 n=225	10-24 18.0±3.6 n=43	24-38 25.7±4.6 n=204
Duration of first verse (msec)	57-230 130.3±41.5 n=31	86-354 193.9±57.2 n=47	161-334 225.1±66.7 n=7	169-532 332.3±84.7 n=38
Duration of following verses (msec)	103-269 155.6±37.7 n=189	111-346 223.9±46.2 n=223	126-299 233.5±45.6 n=43	187-566 313.2±69.4 n=204

song together (as division into series, internal structure of the series, and the change of the amplitude of ticks or pulses) affect the process of song recognition by the female of *C. biguttulus* and other Gomphocerine grasshoppers (VEDENINA & ZHANTIEV 1990). Thus the differences in stridulation between *C. biguttulus* and *C. eisen-trauti*, although they may appear weak to the human observer, might thus be strong enough to prevent a complete fusion of both taxa in zones of contact, as at Pressegger See.

Chorthippus brunneus (THUNBERG, 1815)

Stridulation of *C. brunneus* consists of a sequence of very short verses (fig. 26A-D). The verses usually do not show a distinct pattern of subdivision (fig. 26E-G) and thus consist of a single echeme. They are referred to as echemes by some authors (e.g. BUTLIN et al. 1985, RAGGE & REYNOLDS 1988), but as verses by others (e.g. ELLEGAST 1984). For convenience of comparison with the other species, the term verse is preferred here.

The pulses in a verse of *C. brunneus* (nominate form) are produced by 4-6 up and down strokes of the hind femora. Although both legs are moved with alternating phases, the pulse pattern is maintained by the fact that the second leg stops moving for a while when the first reaches a turning point and thus produces no noise (ELLEGAST 1984). With the exception of the first verse, verse duration is usually constant throughout the song (ELLEGAST 1984).

Verse duration of *C. brunneus* (environs of Erlangen, Germany) varies between about 110 - 190 ms for the first and 170 - 220 ms for the following verses

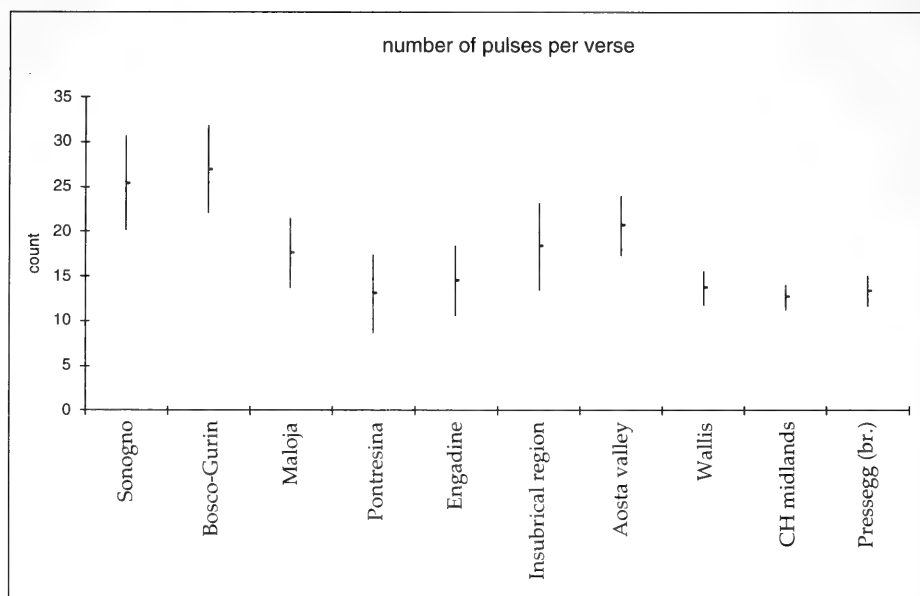


FIG. 27

Number of pulses per verse in populations of *C. brunneus* from the Alps and the Swiss midlands. Means and standard deviations are given.

(means 180-200 ms) (ELLEGAST 1984). The stridulation of *C. brunneus* from the Swiss midlands, Valais, Engadine, and Carinthia agrees quite well with this description (tab. 4). Verses of males from Maloja, the Insubrical Region and the Aosta valley are somewhat longer (fig. 26G) and those from Sonogno and Bosco-Gurin distinctly longer than for nominate *C. brunneus* (fig. 26C-D, H-J; tab. 4). Although both the populations of *C. brunneus* from Maloja and from the Insubrical Region are intermediate between nominate *brunneus* and Ticino-*brunneus* with regard of the verse duration, the former are grouped with Ticino-*brunneus* and the latter with nominate *C. brunneus* on the base of overall characters (i.e. shape of tegmen, coloration). It is however possible that, despite of the similarity of the Maloja population with those of Sonogno and Bosco-Gurin, their similarity resulted from different evolutionary pathways.

The differences in verse length are reflected in the same way when the number of pulses is used as a measure for the verse length (fig. 27). In the mean, *C. brunneus* populations from the Swiss midlands, Valais, Engadine and Carinthia have the shortest verses, those from Sonogno and Bosco-Gurin the longest, and those from Maloja, the Insubrical Region and Aosta valley are intermediate.

If we compare verse duration between *C. brunneus* and *C. biguttulus* or *C. eisentrauti*, it is without question that both the mean and the range of verse duration

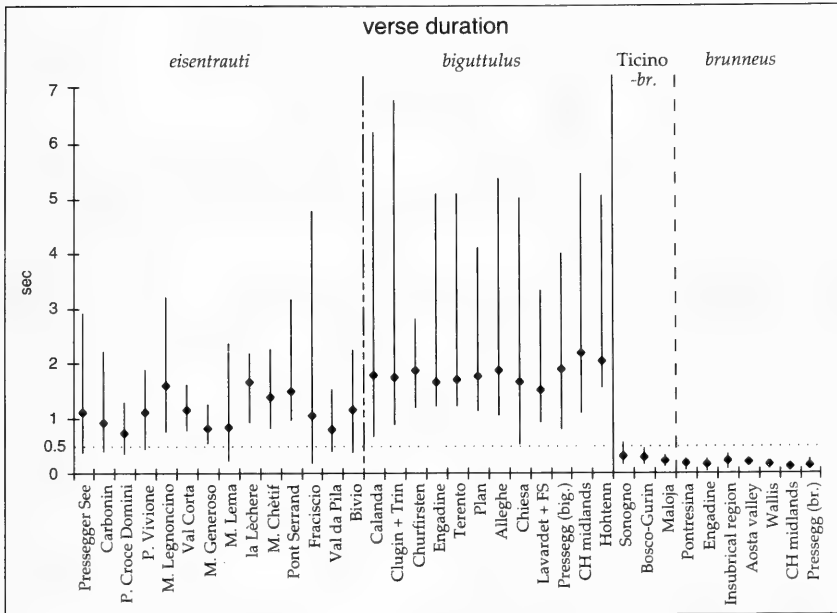


FIG. 28

Duration of verses in songs of *C. biguttulus*, *C. eisenTrauti* and *C. brunneus* from the Alps and the Swiss midlands. Medians and ranges are given.

of nominate *C. brunneus* are distinctly shorter than any verse of *C. biguttulus* or *C. eisenTrauti*. Even if we compare Ticino-brunneus with *C. eisenTrauti*, the mean or median verse duration differs quite distinctly between both taxa (fig. 28). However, due to the high variability, the longest verses of Ticino-brunneus are longer than the shortest verses of *C. eisenTrauti* (fig. 26, 28). Moreover, the echeme-syllable pattern is sometimes indistinct in the preverses of the *C. eisenTrauti* stridulation and, on the other hand, a few of the *C. brunneus* songs show an indication of a pattern of subdivision. As a result the difference in verse duration between *C. eisenTrauti* and *C. brunneus* is also merely a statistical one, although the difference between *C. eisenTrauti* and *C. brunneus* is usually more distinctive than the difference between *C. eisenTrauti* and *C. biguttulus*. The hypothesis that the difference between the stridulation of *C. eisenTrauti* and *C. brunneus* is gradual is supported by observations in laboratory. When males of *C. eisenTrauti* and Ticino-brunneus were kept together in the same cage, they sometimes performed response songs (fig. 29A), which was never observed between males of *C. biguttulus* and *C. brunneus*.

Chorthippus mollis (CHARPENTIER, 1825)

Stridulation of *C. mollis* consists of a prolonged, crescendoing verse (fig. 29B, E). The verse is composed of echemes of continuously increasing intensity and

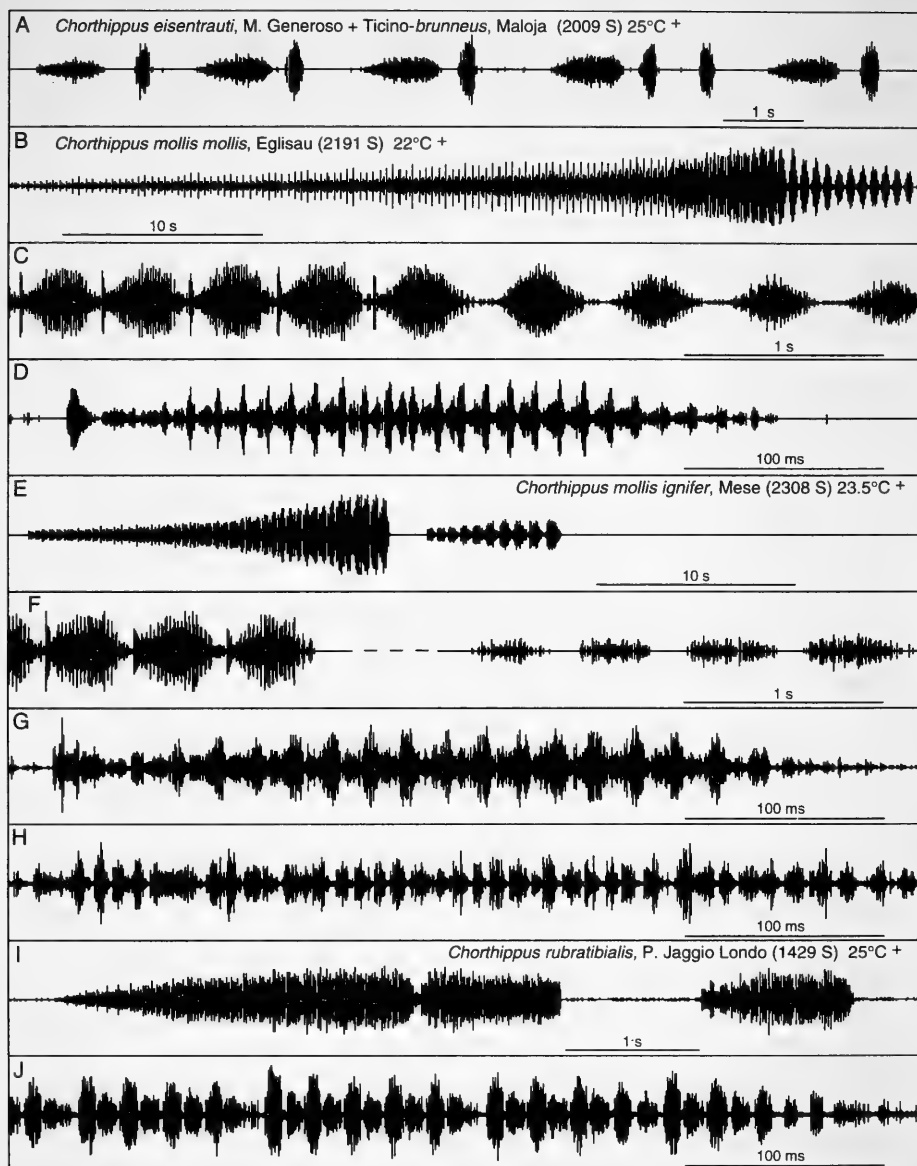


FIG. 29

Oscillograms. A: Response song between a male of *C. eisentrauti* and a male of *Ticino-brunneus*; B-D: *C. m. mollis*; E-H: *C. m. ignifer*; I-J: *C. rubratibialis*; B, E, I: Full songs; E, F: End of song to show the difference between the soft ending in *C. m. mollis* (C) and the loosely added echemes in *C. m. ignifer* (F, the pause between the end of the song and the added echemes shortened in the oscillogram); D, G: Single echemes; H: One loosely added echeme; J: Sectors of verse to show syllable pattern.

TAB. 5

Song characters of *Chorthippus mollis mollis* and *C. mollis ignifer*. Minimum, maximum, mean, standard deviation and number of observations are given. All local populations clustered.

	Number of echemes per verse	Duration of verse (sec)	Endechemes without tick-sound		Loosely added echemes	
			Frequency	Number	Frequency	Number
<i>mollis</i>	20-111 44.1±18.6 n=95	8.0-45.1 16.4±7.4 n=95	78 82%	1-13 5.6±2.3 n=78	3 3%	1-7 3.0±3.5 n=3
<i>ignifer</i>	5-85 32.5±14.5 n=162	1.7-34.5 11.1±5.5 n=162	8 5%	1-9 2.0±2.8 n=8	84 52%	1-11 5.4±2.6 n=84

duration. Each echeme starts with a loud downstroke (tick sound) which is followed by a vibratory phase. The tick sound is produced by only one of the hind femora, the vibratory phase by both femora (ELSNER 1974). During the vibratory phase, the downstroke is louder than the upstroke (ELSNER 1974; see also fig. 29D, G).

Verse duration is variable, lasting from 8 - 45 seconds in the northern and 1.7 - 35 seconds in the southern populations (tab. 5). It is affected and shortened by the presence of other singing males. The shortest songs in the field were observed in the Insubric Region where very high population densities occurred. With the exception of the males from Neuchâtel, mean verse duration in populations from the Swiss midlands and Germany (mean 17.6 sec) was distinctly longer than in populations from the southern Alps (mean 11.1 sec); in the Neuchâtel population, the mean verse duration was only slightly longer (mean 12.9 sec). Even though rivalry songs have been excluded from the analysis, the length of the verses varied such that verse duration alone is not a relevant character for separating the northern from the southern populations.

The same problem arises when the number of echemes per verse is used as a measure for the verse length. Again, the population means of the number of echemes per verse are higher in the northern than in the southern populations, but the total variation ranges from 20 - 111 echemes per verse in the northern, and 5 - 85 in the southern alpine populations. Although the low number of only 5 echemes might be regarded as a characteristic of the rivalry song, one male from Galleno did not produce more echemes even when completely isolated. As with the absolute verse duration there is almost complete overlap in possible verse duration and only the means differ between both taxa.

Apart from verse duration, populations living north of the Alps differ from the southern alpine populations mainly by the tick sound being suppressed near the end of the verse (fig. 29B-C). In the southern alpine populations, the tick sound is kept until the end of the verse and some separated echemes can be loosely added after a pause following the verse (fig. 29E-F). The different song types were already noticed by FABER (1957), however without recognising that they are due to geographic variability. The syllable pattern of the loosely added echemes is not very clear (fig. 29H) and differs thus from the distinct syllable pattern of the echemes produced during the

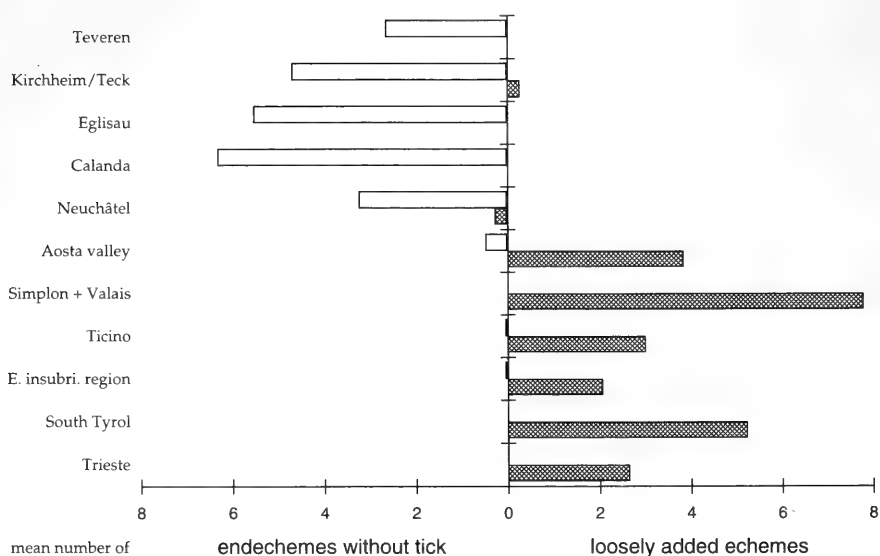


FIG. 30

Differences in stridulation between *C. m. mollis* and *C. mollis ignifer*. Left: Mean number of end-echemes without tick sound; right: Mean number of loosely added echemes following the song.

verse (fig. 29D, G). As the end-echemes of the northern form which lack the tick-sound have the same syllable pattern as the normal echemes, the end-echemes and the loosely added echemes are not just two varieties of the same thing, but represent a distinct difference in behaviour.

We should now test if the differences are constant and reliable characters for separating the northern from the southern form (fig. 30). The northern populations produced between three and six end-echemes without tick sound (population means). The total variation was as follows: 17 of 95 verses ended with a tick sound in the last echeme; in 78 verses the last 2 - 13 echemes were without tick sound. The end-echemes without tick-sound were gradually quietening, thus giving the impression of a soft end of the verse. On the other hand, the southern populations stopped the verse abruptly at the maximum loudness, and after a pause of a few seconds added between 2 and 8 loosely added echemes (population means). The total variation was as follows: 79 of 163 verses without added echemes, 84 verses with 1 - 11 added echemes. There are hardly any exceptions from this difference: 3 of 95 songs in the northern form were with one loosely added echeme, and 8 of 163 verses in the southern form were with one end-echeme lacking the tick sound. Both groups can thus be regarded as valid subspecies on the base of the song characters. The name *Chorthippus mollis ignifer* (RAMME, 1923) is available for the southern alpine form, as males from the type locality (South Tyrol) behave as described above for southern

alpine populations. The range of *C. m. ignifer* probably covers all of the alpine region from southern France to Istra. West of the main alpine ridge, typical songs have been recorded by RAGGE (1981, 1984). North of the main alpine ridge it occurs in the upper Rhone valley (Valais). The occurrence in the upper Rhone valley on one hand and in southern France on the other makes it probable that all populations in the French Alps belong to *C. m. ignifer*. In the Swiss Jura we find already *C. m. mollis*. This subspecies reaches the northern border of the Alps at the Calanda near Chur (Grisons). The subspecific status of the populations from the Inn valley (recorded by NADIG 1991) has not yet been determined. The nominate subspecies occurs also on the Balkan peninsula, as populations from the Danube valley in Serbia and the Durmitor National Park in Montenegro have the soft verse endings typical of *C. m. mollis* (INGRISCH unpublished).

Chorthippus rubratibialis SCHMIDT, 1978

This subspecies does not occur in the area covered by the present paper, but its study might be helpful in understanding the evolution of the song pattern in *C. mollis*. The song consists of a long first verse which can be followed (or not) by one or more short verses (fig. 29I). The first verse is always interrupted once or several times. The verses are composed of echemes with a syllable pattern similar to the situation in *C. eisentrauti*. The number of syllables per echeme is variable but usually higher than in *C. biguttulus* (mean 6.5 syllables per echeme, range 2 - 46 syllables). As there is a tendency that the syllable number per echeme increases towards an interruption (SCHMIDT 1978), the resulting sound resembles somewhat the vibratory sound of *C. mollis*. In two of the four oscillograms figured by SCHMIDT (1978) there is even a very loud pulse at the beginning of the verse and at the restart after the interruption, thus making the oscillogram even more resembling that of *C. mollis*. However, such loud pulses at the beginning of a verse are occasionally also found in *C. eisentrauti* and *C. biguttulus* (see e.g. SCHMIDT 1990 fig. 2).

DISCUSSION

The morphological investigation allowed the separation of the classical species *C. biguttulus*, *C. brunneus* and *C. mollis*, already recognised by RAMME (1920, 1923) or Sychev (1987). But considering all taxa studied, there is a gradual cline in morphological characters from *C. brunneus* via *Ticino-brunneus* and *C. eisentrauti* towards *C. biguttulus*. To contribute to the confusion, the variation of the morphological characters of *C. m. ignifer* overlaps largely with that of *C. m. mollis*, *Ticino-brunneus* and *C. eisentrauti*, and partially also with nominate *C. brunneus* and *C. biguttulus*. In some regions on the southern side of the Alps, where the doubtful taxa *C. eisentrauti* and *Ticino-brunneus* occur, it is often impossible to identify single specimens of the *C. biguttulus* group with certainty if the stridulation was not recorded. On the other hand, as the means of the characters differ between taxa, a tentative distinction

between the taxa in question is usually possible when series of specimens of a population are determined. The greatest taxonomic problems arise in the area between the Adamello Alps and the Aosta valley. Further east, in South Tyrol, the Dolomites, Carinthia and the Alpi Carniche, only two isolated populations of *C. eisentrauti* have so far been discovered, while the Ticino-*brunneus* is absent from that area. Indeed, the Orthoptera fauna in of the Southeastern Alps resembles more that in Central Europe and the central Balkan Peninsula. Both *C. biguttulus* and *C. brunneus* occur here in the nominate subspecies (figs. 31-32).

The real distribution of *C. eisentrauti* is still uncertain. Apart from the type locality in Carinthia, published records refer to local spots on the northern side of the Alps (Berchtesgaden and Calanda), the southern and southeastern side of the Alps, the French Alps, the Apennines and Abruzzi, Istra, Croatia and Bosnia (HARZ 1957, NADIG & STEINMANN 1960, BACCETTI 1958, NADIG 1991, SCHMIDT & BÜHL 1970, MICSIC 1973). However it is probable that several of those records are due to misidentification, as most records are based on morphological characters alone. On the one hand individuals of *C. biguttulus* may have the widening of the subcostal field of the tegmen less distinct and thus resembling the shape of *C. eisentrauti*, and on the other hand large individuals of *C. mollis ignifer* can also look the same as small individuals of *C. eisentrauti*. In the Apennines and Abruzzi confusion with *C. rubratibialis* is also likely, as this taxon was recognised and described as late as 1978.

SCHMIDT & BÜHL (1970) recorded *C. eisentrauti* from the French Alps (Lac du Bourget) on the base of subtle morphological differences compared with *C. biguttulus*. However, DREUX & VOISIN (1974) and VOISIN (1974) expressed some doubt about the validity of *C. eisentrauti* as a distinct species. Indeed, it seems that *C. eisentrauti* is absent from the French Alps, as SCHMIDT & BÜHL (1970) stated that there was no difference in song between *C. biguttulus* and *C. eisentrauti*, and the fig. 4b in SCHMIDT & BÜHL (1970) probably shows *C. biguttulus* and not *C. eisentrauti* as quoted, as the subcostal field of the tegmen is suddenly widened. The records from Croatia and Bosnia (MICSIC 1973) are probably also due to misidentification of an aberrant form of *C. biguttulus*, for the following reason. In Montenegro, in addition to the nominate subspecies, another form of *C. biguttulus* with a large head and the tegminal venation as in *C. eisentrauti* has been found in the Piva and Komarnica canons (INGRISCH & PAVICEVIC in preparation). The stridulation, however, deviates in the opposite direction from *C. biguttulus* than does that of *C. eisentrauti*. The first verse is not shortened but considerably prolonged and the following verses are largely reduced or absent (INGRISCH & PAVICEVIC in preparation).

The distribution of *C. eisentrauti* is thus probably rather restricted to the southern side of the Alps, with the main area between the Adamello Alps and the Aosta valley and two isolated patches in the Dolomites and Carinthia. It is not unlikely that *C. eisentrauti* also occurs in the Piemontese Alps. This should however be verified by additional collecting and song recording. The only place where *C. eisentrauti* was found with certainty north of the main ridge of the Alps is in Bivio. This locality is however not far from the main Alpine ridge. The Bivio population, as

well as those from the Aosta valley, are somewhat closer to *C. biguttulus* than the other populations investigated, as the first verse of a song is often slightly longer than the following.

As all characters, morphological and behavioural, separating *C. eisentrauti* from *C. biguttulus* are gradual, it seems that both taxa are still on the way to differentiation, with the isolating mechanism probably not fully developed. Describing additional taxa on the base of subtle morphological or behavioural differences between regional populations would not be very helpful for understanding the evolution of the *C. biguttulus* group in the Alps.

The populations of *C. eisentrauti* in the Insubrical Region and the Aosta valley are well isolated by the orographical situation of the Alps and the resulting climatic conditions. In the west, north and east they are isolated by high altitude. In the south, they are isolated by the plain of the Po which possibly provides unsuitable climatic conditions, as hardly any population lives below 1200m. It is interesting to observe that *C. biguttulus*, which is otherwise widespread in the Alps, is absent from that area (fig. 31, NADIG 1991). Instead, *C. m. ignifer* is very widespread and common in the Insubrical Region (fig. 33), a fact that led NADIG (1991) to the conclusion that this species is less stenotopic than supposed by former authors. It seems that in the Insubrical Region it occupies at least part of the habitats that are usually inhabited by *C. biguttulus* in other areas (own observations). From South Tyrol eastwards, however, it is much more restricted to xerothermic habitats, similar to the situation with *C. m. mollis* north of the Alps.

The situation of *C. brunneus* in the southern Alps is rather curious. In Carinthia the nominate form exists, as well as in the Insubrical Region at lower elevations. The latter might have invaded through the plain of the Po. Although the number of stridulatory pegs of populations from the Insubrical Region and the Aosta valley is slightly higher and the verse duration longer than in populations of *C. brunneus* from Central Europe, Valais and Carinthia, there is no doubt that they belong to the nominate form. The example shows that local differentiation occurs in the range of this widespread species. Another deviating form of *C. brunneus* was described from South Finland as *C. b. brevis* KLINGSTEDT, 1939. This subspecies also differs in a higher number of stridulatory pegs and by longer verse duration from the nominate form (KLINGSTEDT 1939). The longer verse duration however is due to slower leg movement (PERDECK 1957), while in *C. brunneus* from the Insubrical Region it is due to a higher number of pulses per verse. The differences to nominate *C. brunneus* are most expressed in populations of two isolated valleys of Ticino. They are referred to as *Ticino-brunneus* in this paper. Those populations also deviate in the shape of the tegmen and possess striking red hind tibiae. As all the characters in which these populations deviate from *C. brunneus* are approached to *C. eisentrauti*, it might be that they originate from a stabilised hybridisation between both taxa. The stridulation is similar to that of laboratory hybrids between *C. brunneus* and *C. biguttulus* (see below, PERDECK 1957). A similar form occurs at the Maloja pass which separates the valley of Bregaglia from the Upper Engadine. At only 1815m one of the lowest passages in the

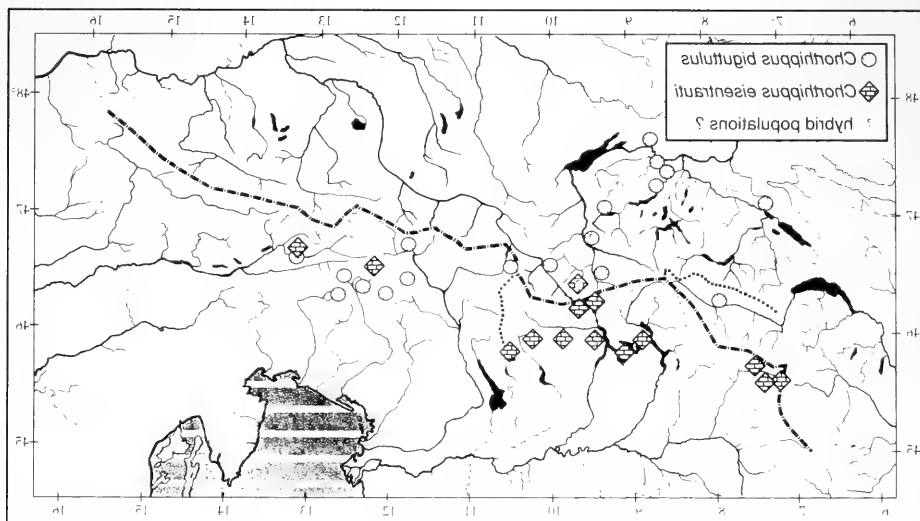


FIG. 31

Distribution map of *C. biguttulus* and *C. eisentrauti* in the Alps based exclusively on the populations studied in this paper. The populations marked with a "?" show intermediate characters between both taxa.

western Alps, this pass connects the Inn valley with the Insubrical Region, i.e. the northern and southern side of the Alps (NADIG 1991). In this area, the situation of the *C. biguttulus* group is very complex, as possibly two zones of hybridisation between different taxa occur: (1) between *C. eisentrauti* and *C. brunneus* via Val da Pila - Maloja - Pontresina, and (2) between *C. eisentrauti* and *C. biguttulus* via Val da Pila - Bivio - Calanda.

The hypothesis that hybridisation between those taxa occurred is supported by the fact that characters of minor importance for species isolation show a cline over a long distance, while characters important for species isolation change rapidly within a narrow zone of contact. In the *C. biguttulus* group, species recognition is mainly based on behavioural and not on morphological characters. Thus morphological characters of *C. eisentrauti* can be found as far as the Calanda population in the upper Rhine valley, which, judging from stridulation, distinctly belongs to *C. biguttulus*. The morphology of the *C. brunneus* population of Pontresina in the Upper Engadine also resembles *C. eisentrauti*, but the song is that of nominate *C. brunneus*. The zone of contact between *C. eisentrauti* and *C. brunneus* is at the Maloja pass. Down from the Maloja pass (Val da Pila), stridulation shows the echeme-syllable pattern of *C. eisentrauti*, up on the Maloja pass, that of *C. brunneus*. But there is a great deal of overlap with regard to the verse length. Thus the different syllable pattern is obviously the most important character for the mating success of the males and thus

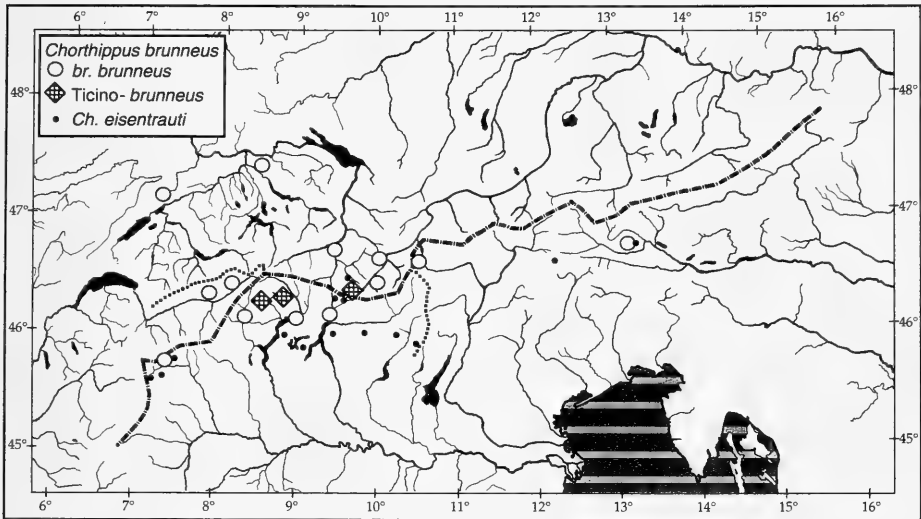


FIG. 32

Distribution map of *C. brunneus* and *Ticino-brunneus* in the Alps based exclusively on the populations studied in this paper. For comparison, the distribution of *C. eisenrauti* is also indicated by small dots.

for the specific isolation between *C. eisenrauti* and *C. brunneus*. On the other hand, the echeme-syllable patterns of *C. biguttulus* and *C. eisenrauti* are identical, apart from the statistical means. Thus the characters separating both taxa can change over a larger area. Indeed, the Bivio and the Calanda populations mediate between *C. eisenrauti* and *C. biguttulus*. One might thus think of *C. eisenrauti* as a geographical race of *C. biguttulus* (see below).

Other areas of contact between *C. eisenrauti* and other taxa exist in Carinthia and the Dolomites. In Carbonin (Dolomites), the population is somewhat isolated, as no other taxa of the *C. biguttulus* group live in the same locality. The closest populations of *C. biguttulus* live in Toblach and Cortina (JACOBS 1957), that is along the valleys, 15 km north or 18 km south. At Pressegger See, *C. eisenrauti* lives in close contact with other members of the group. Only 100-200 m of altitude covered with pine forest or the rocky slopes of a quarry separate *C. biguttulus* from *C. eisenrauti*. Thus hybridisation between the two could be possible. But the population means of both morphological and acoustical characters of the Pressegger See populations of *C. eisenrauti* and *C. biguttulus* differ quite distinctly from each other, thus indicating that isolation between the two populations is strong enough to prevent a fusion between these forms. The Pressegger See population of *C. eisenrauti* also lives mixed with nominate *C. brunneus* along a forest road higher on the same mountain. There is no hint that they interbreed in this locality.

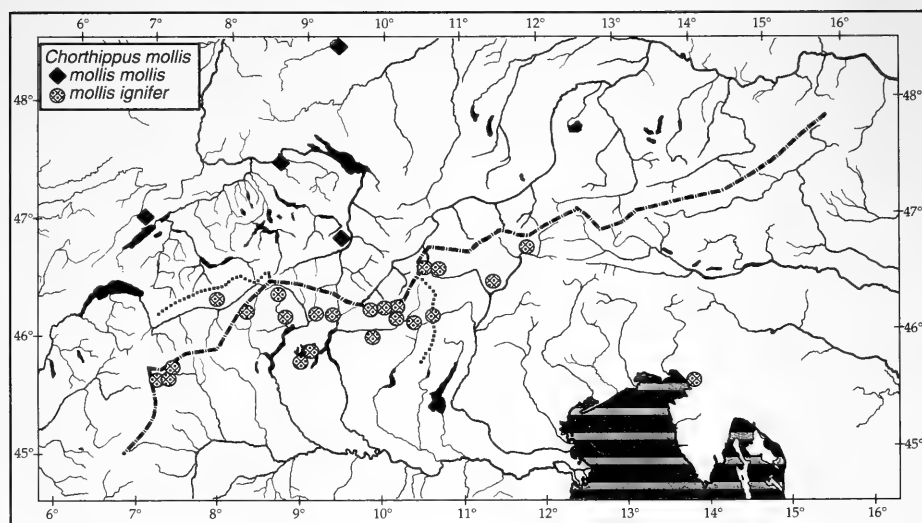


FIG. 33

Distribution map of *C. m. mollis* and *C. m. ignifer* in the Alps and adjacent areas based exclusively on the populations studied in this paper.

As the species of the Gomphocerinae are mainly isolated by behavioural characters, we must now look for the features and differences of the songs of the taxa considered. It was shown before that the difference in stridulation between *C. biguttulus* and *C. eisentrauti* is a mere statistical one concerning the population means, and the same of course holds true for the difference between *C. brunneus* and Ticino-brunneus. Moreover, the difference between *C. eisentrauti* and Ticino-brunneus is also not very great as the ranges of the verse duration overlap between both taxa. Stridulation of Ticino-brunneus resembles the descriptions of Perdeck (1957) for hybrids between *C. biguttulus* and *C. brunneus*. As males of *C. eisentrauti* and Ticino-brunneus can react to the song of the opposite taxon with response songs, one might speculate that the difference in stridulation is not so great as one might conclude from the different syllable pattern.

Stridulation of *C. eisentrauti* is the most variable of the group discussed. The song is a sequence of loosely grouped verses, arranged into echemes. The verses vary in duration from the respective values of Ticino-brunneus to those of *C. biguttulus*, without reaching the extreme values of both taxa. The syllable pattern of the echemes is also variable. It varies from low-syllabic echemes (two or three-syllabic) to multi-syllabic echemes (up to 44 syllables). The three-syllabic echemes are identical with the pattern in most echemes of *C. biguttulus*, with the first syllable of an echeme usually accentuated and the up- and down-movements of the postfemur resulting in

subequal loudness of pulses. The multi-syllabic echemes often show a pattern with quiet up and loud down movements as in the echemes of *C. mollis*.

Stridulation of *C. biguttulus* differs from that of *C. eisenrauti* only in two points: (1) it is more regular with regard to both verse number per song and syllable number per echeme, and (2) the verses are longer. The difference in verse duration concerns mainly the first verse. On the other hand, stridulation of *C. brunneus* differs from that of *C. eisenrauti* by shorter verse duration and by a different syllable pattern.

The way in which two males time their songs relative to each other is usually regarded as another difference in stridulation between *C. brunneus* and *C. biguttulus*. Two responding males of *C. brunneus* alternate their verses, while those of *C. biguttulus* usually overlap their verses. This difference however is also gradual, as in *C. eisenrauti* we can observe both alternating response songs and overlapping response songs when the males perform longer verses. Even males of *C. biguttulus* can alternate in populations that perform shorter verses (fig. 16).

Moreover, one might even suppose that the stridulation of *C. mollis* is derived from a pattern that was similar to that of *C. eisenrauti*. We have seen that the syllable pattern in the stridulation of *C. mollis* with a quiet up and a loud down movement of the postfemur can also be found in some of the long echemes of *C. eisenrauti*. The deviating characters of *C. mollis* would then be that the number of echemes per verse was reduced to one, but the number of verses greatly increased and the pauses between the verses omitted. If so, the "echemes" in the song of *C. mollis* would be equivalent to the verses in *C. eisenrauti*. The homology of the echemes of *C. mollis* with the verses of *C. biguttulus* was already stated by HELVERSEN & HELVERSEN (1975) and HELVERSEN & ELSNER (1977). Another typical feature of the stridulation of *C. mollis* is the tick-sound at the beginning of the echemes (verses), produced by a loud down movement of one hind leg (ELSNER 1957). A loud pulse is sometimes also produced at the beginning of a verse of *C. eisenrauti* or *C. biguttulus* (figured e.g. in SCHMIDT 1990). If we suppose that the echemes in *C. mollis* are equivalent to the verses in *C. biguttulus* and *C. eisenrauti*, the tick sound might be derived from this initial pulse.

A transient form of song occurs in *C. rubratibialis* from the Apennines. At the beginning of stridulation, two or more verses are appended, and thus resembling the situation in *C. mollis*, while the rest of the song and the syllable-echeme pattern of the verses resemble those of *C. biguttulus* and *C. eisenrauti* (SCHMIDT 1978, RAGGE 1987).

A hypothetical scheme for the evolution of the members of the *C. biguttulus* group from a common ancestor is presented in fig. 34. This is mainly based on the hypothetical deviation of stridulation. The widening of the costal fields of the tegmen possibly coincides with the change of stridulation and/or differences in habitat preference, as the widening of the costal fields provides better means of resonance and thus better propagation of sound in a grassland habitat.

We must now answer the question about the taxonomic status of *C. eisenrauti*. If *C. eisenrauti* was restricted to the Insubrical Region from which *C. biguttulus* is absent (fig. 31, NADIG 1991), we could well think of *C. eisenrauti* as a geographical

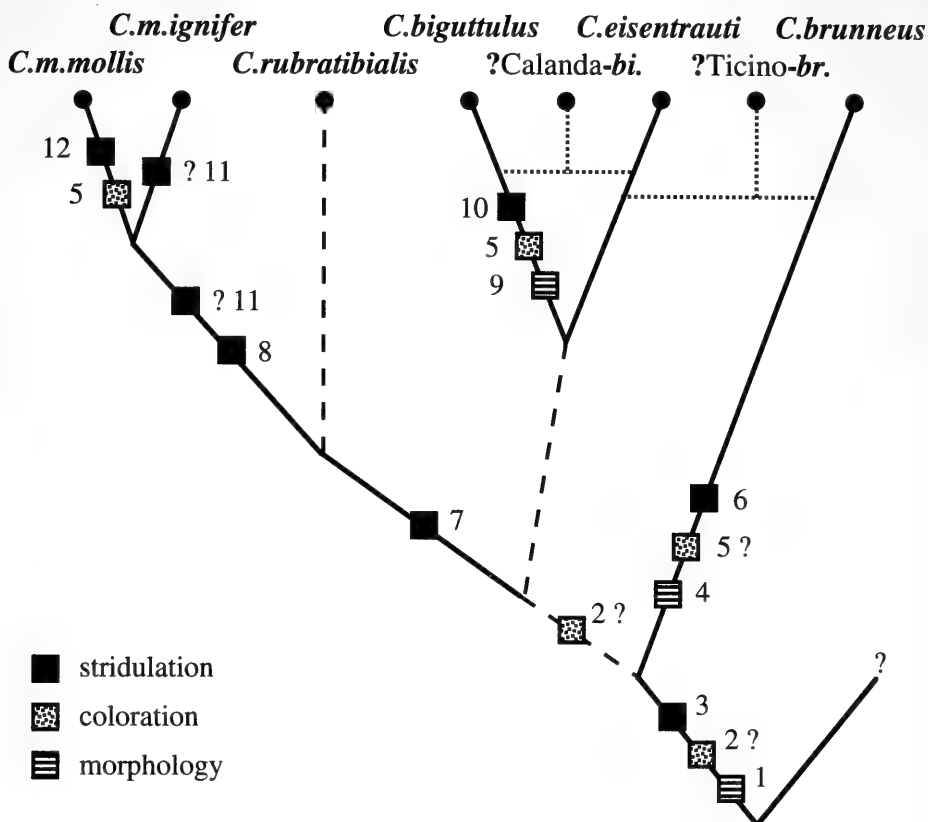


FIG. 34

Hypothetical scheme of the evolution of the taxa of the *C. biguttulus* group as occurring in the Alps (*C. rubratibialis* is included for convenience) based on behavioural and morphological characters. The occurrence of hybrid populations is uncertain (indicated by dotted lines). The characters are as follows: 1 = moderately widened tegmen (C- + SC-fields); 2 = striking red posttibiae; 3 = numerous short verses, separated by pauses, echemes with varying number of syllables (2 - 44), alternating singing of two males; 4 = narrowing of tegmen (greater flight capacity), number of stridulatory pegs reduced; 5 = loss of red coloration of hind tibiae; 6 = shortening of verses, loss of echeme-syllable pattern; 7 = number of long-syllabic echemes increased, attached verses at beginning of song; 8 = number of echemes reduced to one per verse, verses attached in high numbers, tick-sound; 9 = greater widening of C- + SC fields (resonator); 10 = prolonged verse duration (mainly first verse) combined with a reduction of verse numbers, echeme-syllable structure becomes regular; 11 = abruptly ending song, loosely added echemes; 12 = gradually quietening end of song.

race, i.e. subspecies of the latter. However the populations in Carbonin and Pressegger See extend the range of *C. eisenrauti* far into the range of *C. biguttulus*. For this reason we can exclude a subspecific status. Moreover, the analyses in this paper give no hint that the populations from the Insubrical Region differ from that from Pressegger See or Carbonin. The Carbonin population was described as a aberrant form of *C. biguttulus* (JACOBS 1957), but there are no differences from the Pressegger See populations of *C. eisenrauti*, and it thus belongs to the same taxon. Thus, *C. eisenrauti* is more than just a local variant of *C. biguttulus*, as it could have been if it was restricted to Pressegger See.

There are two more possibilities: (1) it is a stabilised hybrid between *C. biguttulus* and *C. brunneus*, or (2) it is a relic of the common ancestor of the *C. biguttulus* group. In the latter case one must admit of course that it has further evolved, but conserved many of the primitive characters of the group. The intermediate character of *C. eisenrauti* between *C. biguttulus* and *C. brunneus* would support both hypotheses. There are however some arguments against the first hypothesis. The area of *C. eisenrauti* is rather wide, although much more restricted than those of both other species. And, although one cannot exclude that *C. eisenrauti* was interbreeding with one or the other species in some areas, or still is doing so, it is reproductively isolated in other areas. For example, *C. eisenrauti* lives sympatrically with *C. brunneus* at Pressegger See, but there is obviously a hybrid-zone between both taxa via the Maloja pass. Moreover, it would be difficult to explain how the Pressegger See and Carbonin populations could retain their identity within the range of *C. biguttulus* if they were only hybrids. PERDECK (1957) has shown that male F1 hybrids of *C. biguttulus* x *C. brunneus* have almost no mating success as their intermediate song is not recognised by the females of either of both parent species. It has also been shown that mate selection of females of *C. biguttulus* is very selective. In studies with intact and one-leg-singers or with intact and muted males, females preferred the intact males (KRIEGBAUM 1989, KRIEGBAUM & HELVERSEN 1992). Behavioural studies on the mate selection of females of *C. eisenrauti* and *C. biguttulus* with males of their own and the opposite taxon showed that usually the females selected males of their own taxon for mating, although some exceptions occurred, and in one repetition females of *C. biguttulus* preferred males of *C. eisenrauti* (INGRISCH & BASSANGOVA 1995). It would be interesting to find out what makes the selective difference between the choice of females of *C. eisenrauti* and *C. biguttulus*. A hybrid origin of *C. eisenrauti* is thus not very likely, but it cannot be excluded by the evidence at hand with certainty. On the other hand, the second possibility cannot be proven either. But I would like to present it as hypothesis for discussion on the evolution of the *C. biguttulus* group in the Alps. Until more evidence is obtained, it is best to treat *C. eisenrauti* as a sister species of *C. biguttulus* in which (1) many of the primitive characters of the *C. biguttulus* group are conserved and (2) speciation is not yet completed so that hybridisation might locally still occur.

The climatic situation in the Alps changed drastically several times during the ice ages (see SCHWEIZER 1991). Local areas free of ice at the southern side of the Alps

(Massifs de Refuge) possibly allowed some grasshopper species to survive in the vicinity of the Alps even at the greatest extent of glaciation (NADIG 1968, 1989). These refuges at the southern side of the Alps and in other areas of Italy were well separated from refuges in other parts of Europe by the glaciation of the Alps.

Invasion and regression of taxa of the *C. biguttulus* group coincided with the expansion and retreat of the ice. Thus we must expect several waves of invasion into the Alps. Evolution of the taxa of the *C. biguttulus* group occurred during this time, as this is a group of evolutionary young species with speciation still in progress. Some of the earlier invaders possibly survived in the refuges south of the Alps. As a new wave of invasion occurred, the populations with their own evolutionary history were mixed up again if the reproductive barriers were not fully evolved. In other populations, speciation could have proceeded far enough that hybridisation was not longer possible. With the next expansion of the ice the "evolutionary game" was repeated. Due to the orographic situation of the Alps, some populations might have been isolated for an extended period of time as some of the later invaders might not have had enough time to colonise the whole area or were prevented from doing so by the orographic situation. For example, the modern form of *C. biguttulus* is still absent from the Insubrical Region. The relative isolation of that area has been discussed above. It is not strange that the questionable taxa which possibly represent relics of primary invaders are mainly found here.

The modern forms of the *C. biguttulus* group which live north of the Alps agree with regard to the morphological characters and stridulation with populations on the Balkan Peninsula, e.g. Durmitor in Montenegro (INGRISCH & PAVICEVIC in preparation). It is plausible that they evolved in the same centre of origin and that the colonisation of northern Central Europe after the retreat of the ice was from the Balkan Peninsula. For the same reason, the populations of *C. biguttulus* and *C. brunneus* from the south eastern Alps agree in their subspecific status with the northern Central European forms. This however is not so with *C. mollis*. We can find the subspecies *C. m. ignifer* from southern France to Istra along the south side of the Alps, and along the West of the Alps this subspecies colonised even areas north of the main Alpine ridge along the valley of the river Rhone. From those biogeographical data, and if we suppose the *C. mollis* song as being derived from the *C. eisenrauti* song via a step similar to that of *C. rubra-tibialis*, it is more probable that *C. mollis* evolved in an Italian refuge. And, colonisation of northern Central Europe and the Balkan peninsula took place only after another step of subspeciation into the two subspecies presently recognised.

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